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Ocean Springs, Mississippi

Gulf Research Reports

Volume 7 | Issue 1

January 1981

Morphometrics of the Burrowing Clam *Diplothyra smithii* Tryon

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MORPHOMETRICS OF THE BURROWING CLAM *DIPLOTHYRA SMITHII* TRYON[1]

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ABSTRACT   *Diplothyra smithii* Tryon, a small bivalve mollusk, is a common inhabitant of the calcareous shell material of the American oyster, *Crassostrea virginica* Gmelin. Large populations of this clam are found on commercial oyster reefs in the western portion of Mississippi Sound. Several aspects of the population of *D. smithii* in Mississippi Sound were examined.

On the Pass Marianne Reef, 71% of the live oysters and 44% of the dead shells were infested with *D. smithii*. The mean number of clams removed from valves of live oysters was 22.1 ± 1.7 (range, 1–109; N = 146). Infested dead shells had a mean number of 23.7 ± 2.6 (range, 1–103; N = 75) clams per shell.

Clams from live and dead shells indicated monthly variations in morphological stages. During January through April, clams were predominantly immature. In late spring and early summer, clams matured morphologically. In May and June, the majority of clams were mature. Immature clams from early and midsummer spawnings appeared in July and August.

Mean lengths and heights of clams with and without a callum and the monthly changes in those dimensions were determined for clams from live and dead shells. All clams from live oysters had greater mean dimensions and size ranges than clams from dead shells. Female clams were significantly larger than nonfemale clams from live oyster shells; females from dead shells were significantly larger than nonfemale clams in length only.

INTRODUCTION

Information on population dynamics of invertebrate organisms is essential to adequately appraise the role of specific organisms within an estuarine ecosystem. Although numerous population studies have been conducted on burrowing bivalve species from sand or mud substrata (Fraser 1967, Moore and Lopez 1969, Holland and Dean 1977), few have been conducted on rock- or shell-burrowing bivalves.

Diplothyra smithii Tryon is a small bivalve mollusk specialized for burrowing into calcareous shell material, particularly the American oyster, *Crassostrea virginica* Gmelin. Despite the high incidence of *D. smithii* in oysters on the northern coast of the Gulf of Mexico, very little information concerning the percentage of shells infested, the density of clams per shell, or the morphology, size, or sex of those clams is available. Collier ([unpublished] cited by Hopkins 1949) attempted to survey the *D. smithii* population in Texas; however, only a few unpublished reports were available.

Most surveys have reported only the prevalence of *D. smithii* and have made observations on oyster-shell damage (Moore 1899, Cary 1906, Galtsoff et al. 1935, Higgins 1940, Federighi and Collier [unpublished] cited by Hopkins 1949). Higgins (1940), Menzel (1950), Galtsoff (1964), and Harry (1976) reported densities of *D. smithii* within single oyster valves. Information on the size of *D. smithii* can be found in the original description (Tryon 1862), in taxonomic monographs (Bartsch and Rehder 1945, Turner 1955), and in numerous guides to marine mollusks (Abbott 1974,

Andrews 1977). None of those reports presented series of measurements.

Diplothyra smithii is characterized by a change in shell morphology as it develops from an immature to a mature form. Turner (1954) described the morphological stages and their characteristic behavioral, structural, and functional patterns for pholads in general. Specific information on the morphological stages of *D. smithii* has not been reported.

The objective of this study was to obtain information on the oyster shell as a substratum inhabited by *D. smithii*, the percentage of shells infested (prevalence), densities of clams within oyster shells, and information on the morphological stages, sizes, and sex of *D. smithii*.

MATERIALS AND METHODS

Field Sampling

Samples of live and dead oyster shells containing *D. smithii* were dredged monthly from January through August 1976, and infrequently during 1975, 1977, and 1978, from Pass Marianne Reef. This reef is located 2 miles due south of Pass Christian, Mississippi, in the vicinity of navigation marker 7M in Mississippi Sound. Surface salinity and temperature were also recorded on each sampling date.

Laboratory Procedures: Percentages of Shells Infested

The percentage of live and dead oyster shells infested with *D. smithii* was determined by placing individual live oysters and dead shells in a large fiberglass trough of sea water which was heated to approximately 30°C to drive off oxygen. This forced the clams to extend their siphons and facilitated identification of infested shells.

Oyster Shell Measurements

To adequately describe the substrata inhabited by

D. smithii, live and dead shells were examined. Ten live oysters were arbitrarily selected and shucked. Measurements were made with vernier calipers of left and right valves for height and length (to the nearest 1.0 mm), and thickness in the umbo region and at the ventral margin (to the nearest 0.1 mm). Heights and lengths of ten dead shells also were measured. Because of the eroded nature of dead shells, only a single measurement of thickness was made midway between the dorsal and ventral margins.

Number of Diplothyra smithii per Oyster Valve

From the infested shells, ten live oysters and ten dead shells were arbitrarily selected to determine the densities of burrowing clams within the shells. The numbers of siphon holes in a given dead valve were counted. Each valve of live shells was divided into four quadrants through the dorso-ventral and anterio-posterior midpoints, and the number of siphon holes within each quadrant was counted. Quadrant densities were examined to relate the number of clams to thickness, i.e., age, of the shell. The procedure that was followed and the orientation of the quadrants were basically those described by Galtsoff (1964).

Cross products of shell heights and lengths were used to compute relative shell areas which were correlated with the number of clams present. This was determined to be the most feasible method for computing area, since the actual shell areas were not calculated prior to destruction of shell valves to obtain *D. smithii.*

Burrowing clams were collected from oyster shells cracked open with a hammer. All clams visible to the naked eye were removed by successively breaking and picking through the shell fragments.

Morphological Stages of Diplothyra smithii

Clams were separated into three stages of morphological maturity based on callum development to determine relationships between the season and the stage of maturity. Clams without a callum were morphologically immature and in the active burrowing stage. These were characterized by the presence of a wide pedal gape through which the foot protruded, unprotected by a shell covering. Clams with a partial callum varied from those with a thin shell just beginning to grow over the pedal gape to those having a thin, pliable callum almost completed but still allowing valve articulation about the umbonal-ventral axis. The mature stage was characterized by a complete callum. At that stage, the pedal gape was completely covered by shell material with no valve articulation.

Sizes of Diplothyra smithii

Lengths and heights of all clams were measured to relate size to substratum, to morphological stage, and to sex. Length was the greatest anterior-posterior dimension of the shell. Height was the length of the umbonal-ventral sulcus, a line from the umbo to the ventral shell margin (Evans 1968).

Clams were measured to the nearest 0.1 mm using an ocular micrometer and a steroscopic binocular microscope. To determine the monthly population structure, length-frequencies for all clams from a given month were plotted to indicate the percentage of clams within 2 mm size classes.

Sex: Mature Females

Numbers and sizes of mature females in each monthly sample were compared with numbers and sizes of all other clams. Only ovigerous females were recorded because they were recognized easily by the presence of pink gonadal material.

Statistical Notation

Numerical and size measurements in text and tables herein are represented as mean ± one standard error of the mean. The sample size is given in parentheses. All tests of significance were done using Analysis of Variance (ANOVA). Only probability levels exceeding 95% were reported.

RESULTS

Oyster Shell Measurements

From live shells, the mean height of left valves, 83 ± 1.5 mm (73), was significantly larger than the mean height of right valves, 77 ± 1.4 mm (73). The mean length of left valves, 64 ± 1.1 mm (73), also was significantly larger than the mean length of right valves, 59 ± 1.0 mm (73). There was no significant difference between the thickness of left valves, umbo: 8.9 ± 0.2 mm (73), mid-ventral: 2.6 ± 0.1 mm (73); and right valves, umbo: 8.8 ± 0.3 mm (71), mid-ventral: 2.6 ± 0.1 mm (71). Dead shells had a mean height of 82 ± 2.5 mm (76), a mean length of 49 ± 1.0 mm (76), and a mean shell thickness of 5.7 ± 0.2 mm (75).

Percentage of Shells Infested with Diplothyra smithii

Seventy-one percent of the live oysters and 44% of the dead shells were infested with *D. smithii* (Table 1).

Density of Diplothyra smithii per Infested Oyster Valve

There was no significant difference between the mean densities of clams in the left and right valves of live oysters; left: 22.6 ± 2.5 mm (73); right: 21.6 ± 2.2 mm (73); combined: 22.1 ± 1.7 mm (146). The maximum density was 109 clams per shell. Fifty-seven percent of the live shells examined contained between 1 and 20 clams. There were significantly greater numbers of clams near the umbo in the dorsal quadrants of live shells. Anterior quadrants had mean densities of 9 clams per quadrant compared with mean densities of 2 clams per quadrant in the ventral quadrants (Table 2).

Dead shells had a mean density of 23.7 ± 2.6 clams per valve, and a maximum number of 103 clams per valve. Fifty-one percent of the dead shells had between 1 and 20 clams present.

TABLE 1.

Numbers and percentages of live oysters and dead shells infested with *Diplothyra smithii* from Pass Marianne Reef, 1976 and 1977.

Month	Live Oysters			Dead Shells		
	With *D. smithii*	Without *D. smithii*	Total	With *D. smithii*	Without *D. smithii*	Total
February 1976	140	13	153	–	–	–
April	45	22	67	77	98	175
May	–	–	–	38	148	186
June	9	46	55	–	–	–
July	–	–	39	118	146	264
August	–	–	43	82	62	144
September	–	–	22	149	86	235
February 1977	15	6	21	53	108	161
Total	209	87	400	517	648	1165
Mean	52	22	57	86	108	194
Range	9–140	6–46	21–153	38–149	62–148	148– 264
Percentage	71	29	–	44	56	–

TABLE 2.

Number of *Diplothyra smithii* located within each of four quadrants of live oyster shells from Pass Marianne Reef.

Quadrant	Mean Number Removed	(N)	Range
Dorsal Anterior	9.3 ± 0.8	(136)	0–53
Dorsal Posterior	8.9 ± 0.7	(136)	0–41
Ventral Anterior	2.2 ± 0.3	(136)	0–20
Ventral Posterior	2.2 ± 0.2	(136)	0–11

The mean densities of clams per infested valve were similar for both live and dead shells, and the proportion of valves containing equivalent numbers of clams also was similar for both live and dead shells. There was a positive correlation between the number of clams and the size of the shell for both live shells ($r^2 = 0.1084$; N = 146) (Figure 1), and for dead shells ($r^2 = 0.2215$; N = 75) (Figure 2).

Morphological Stages of Diplothyra smithii

Monthly frequencies for the presence of morphological stages of *D. smithii* were similar from both live and dead shells except during July and August (Figures 3 and 4). During the first four months of 1976, 60 to 90% of the clams were present in the immature stage in both live and dead shells. Live shells had 10 to 20% more immature clams than dead shells. In April, there was an increase in the number of mature clams in both live and dead shells, and in May and June, 70 to 90% of the clams examined had a callum. In July and August, differences were found between the morphological stages present in live and dead shells. In live shells 70% of the clams had a callum present; however, in dead shells 80% were without a callum.

Sizes of Diplothyra smithii

Clams from live shells were larger than clams from dead shells (Tables 3–6). Clams from live shells also had wider ranges for both length and height measurements. Mean lengths for clams with a callum were larger than the mean lengths for clams without a callum from both shell types (Figures 5 and 6).

Mean lengths and heights for each morphological stage are given for each month (January through August 1976) in Tables 3 and 4 for clams removed from live shells, and in Tables 5 and 6 for clams removed from dead shells. Clams removed from live shells had a total mean length of 6.8 ± 0.4 mm (1,567) for clams with a callum, and a total mean length of 3.9 ± 0.0 mm (1,451) for clams without a callum (Table 3). Clams removed from dead shells had a total mean length of 5.5 ± 0.1 mm (724) for clams with a callum, and a total mean length of 3.0 ± 0.0 mm (917) for clams without a callum (Table 5). The greatest recorded length was 11.4 mm (Table 5).

Diplothyra smithii: Length-Frequencies

Changes in length-frequencies of the sample population of *D. smithii* throughout an 8-month period from live and dead shells are shown in Figures 7 and 8. There was a progressive shift in increasing length of clams from January through June for clams from both live and dead shells. With recruitment of young individuals during July and August, an increase in the percentage of clams was observed in the smaller length intervals. Changes in length-frequency were more pronounced for clams removed from dead shells than for clams removed from live shells.

Sex: Mature Females

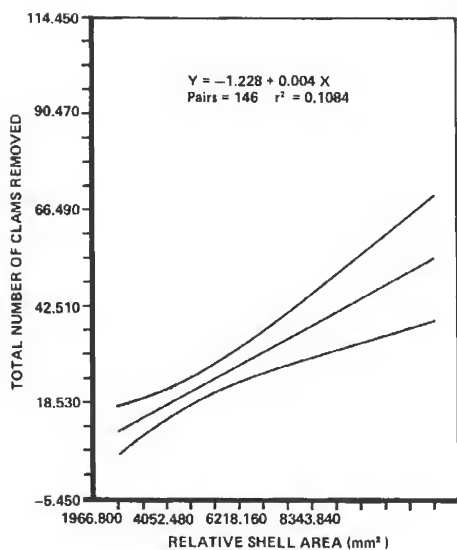Means and ranges for lengths and heights of females from live and dead shells, both with and without a callum,

Figure 1. Relative area (length × height) of live shells compared with the number of *D. smithii* removed from the shells.
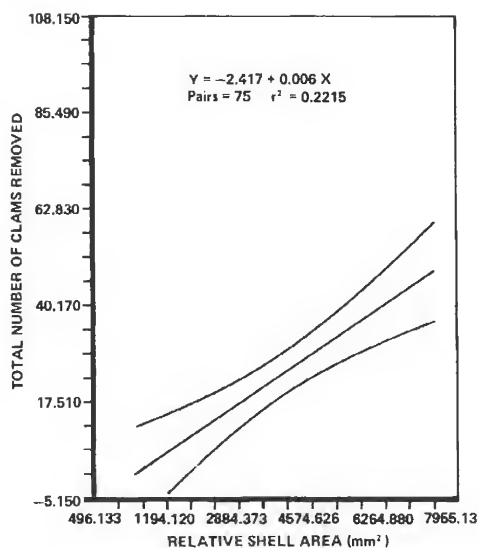

Figure 2. Relative area (length × height) of dead shells compared with the number of *D. smithii* removed from the shells.

Without callum With partial callum With callum   Without callum With partial callum With callum
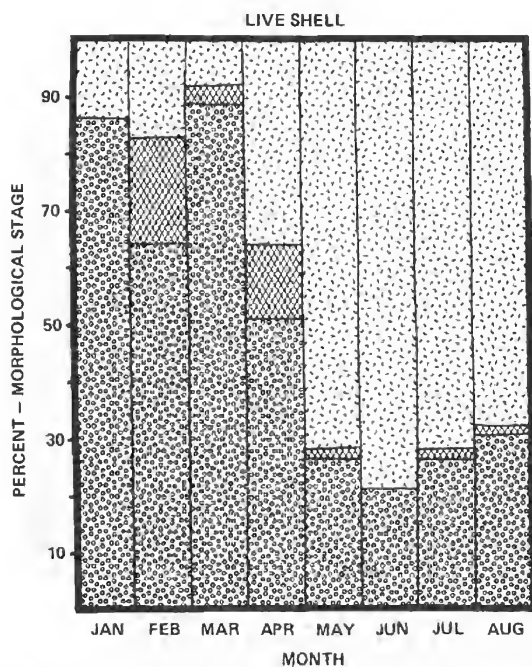

Figure 3. Percentage of clams present in each of three morphological stages for clams examined monthly, January–August 1976, from live shells.
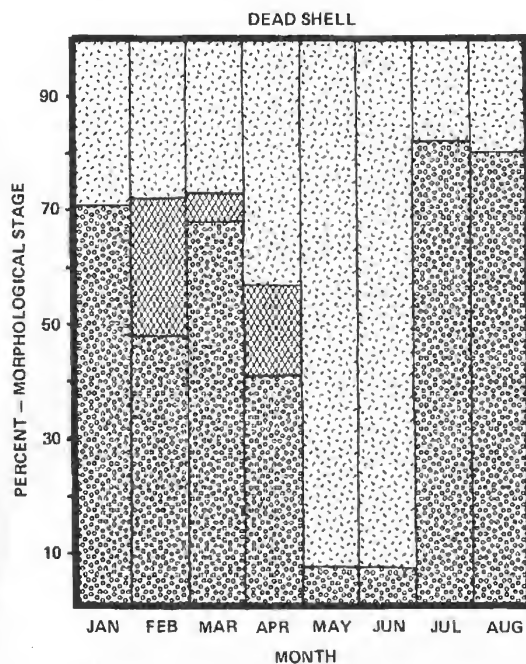

Figure 4. Percentage of clams present in each of three morphological stages for clams examined monthly, January–August 1976, from dead shells.

TABLE 3.

Mean lengths for each of three morphological stages of *Diplothyra smithii* removed from live shells monthly, January–August 1976.

Month	With Callum			With Partial Callum			Without Callum		
January	6.3 ± 0.2	(3.2– 9.5)	40*		0		3.8 ± 0.1	(1.4–9.2)	249
February	5.7 ± 0.3	(1.2–11.0)	57	6.5 ± 0.2	(3.1–8.7)	62	3.9 ± 0.1	(1.2–9.7)	207
March	6.2 ± 0.3	(2.9– 8.7)	29	6.5 ± 0.5	(4.0–8.7)	9	4.4 ± 0.1	(1.4–8.7)	310
April	6.0 ± 0.1	(2.4– 9.7)	150	6.1 ± 0.2	(3.5– 8.7)	56	4.1 ± 0.1	(1.4–8.8)	210
May	6.5 ± 0.1	(3.2–10.5)	292	5.7 ± 0.9	(3.8–8.0)	4	4.0 ± 0.1	(1.6–8.0)	107
June	7.0 ± 0.1	(3.1–10.7)	299	6.1 ± 0.2	(3.9–9.1)	43	4.8 ± 0.1	(2.7–9.2)	77
July	6.7 ± 0.1	(2.9 –11.0)	276	6.8 ± 1.0	(3.9–8.6)	4	2.7 ± 0.2	(0.8–7.1)	103
August	7.3 ± 0.1	(3.2–11.0)	424	8.1 ± 0.4	(6.6–8.9)	6	3.0 ± 0.1	(1.0–8.4)	194
Total	6.8 ± 0.0	(1.2–11.0)	1567	6.3 ± 0.1	(3.1–9.1)	184	3.9 ± 0.0	(0.8–9.7)	1457

*Mean (mm) ± 1 standard error (range), N.

TABLE 4.

Mean heights for each of three morphological stages of *Diplothyra smithii* removed from live shells monthly, January–August 1976.

Month	With Callum			With Partial Callum			Without Callum		
January	4.6 ± 0.2	(1.9–6.8)	40*		0		2.7 ± 0.1	(1.0–6.6)	249
February	3.9 ± 0.2	(1.0–7.1)	57	4.4 ± 0.1	(1.9–6.0)	62	2.8 ± 0.1	(1.0–6.7)	207
March	4.1 ± 0.2	(2.4–5.9)	29	4.7 ± 0.3	(3.0–6.0)	9	3.4 ± 0.1	(1.0–7.0)	310
April	4.1 ± 0.1	(1.6–6.6)	150	4.3 ± 0.1	(2.3–6.0)	56	3.1 ± 0.1	(1.2–7.8)	210
May	4.4 ± 0.0	(1.8–7.1)	292	4.1 ± 0.5	(3.1–5.5)	4	3.1 ± 0.1	(1.4–5.3)	107
June	4.5 ± 0.0	(2.0–6.6)	299	4.1 ± 0.1	(2.1–5.8)	43	3.7 ± 0.1	(1.7–6.1)	77
July	4.4 ± 0.0	(1.9–7.3)	276	4.4 ± 0.5	(3.0–5.3)	4	2.1 ± 0.1	(0.5–5.0)	103
August	4.8 ± 0.0	(2.1– 7.6)	424	5.5 ± 0.2	(5.1–6.5)	6	2.3 ± 0.1	(1.0–6.3)	194
Total	4.5 ± 0.0	(1.0–7.6)	1567	4.3 ± 0.1	(1.9–6.5)	184	2.9 ± 0.0	(0.5–7.8)	1457

*Mean (mm) ± 1 standard error (range), N.

TABLE 5.

Mean lengths for each of three morphological stages of *Diplothyra smithii* removed from dead shells monthly, January–August 1976.

| Month	With Callum			With Partial Callum			Without Callum		
January	3.6 ± 0.3	(3.3– 3.9)	2*		0		3.7 ± 0.2	(1.9–6.0)	50
February	5.3 ± 0.2	(2.0– 9.1)	66	5.5 ± 0.2	(2.9–8.2)	56	3.5 ± 0.1	(1.3–8.4)	110
March	5.0 ± 0.1	(1.9– 7.0)	62	4.5 ± 0.4	(2.9–6.9)	11	3.7 ± 0.1	(1.4–9.2)	154
April	5.3 ± 0.1	(2.2– 8.0)	103	4.9 ± 0.2	(1.6–7.4)	40	3.3 ± 0.1	(1.4–7.4)	99
May	5.7 ± 0.1	(3.0– 9.4)	221		0		3.7 ± 0.3	(1.6–5.1)	16
June	6.1 ± 0.1	(2.3–11.4)	160		0		4.2 ± 0.4	(2.0–6.1)	10
July	4.8 ± 0.2	(1.9–10.0)	70	5.4 ± 0.0	(5.4–5.4)	1	2.3 ± 0.0	(0.8–6.6)	314
August	4.8 ± 0.3	(1.9– 8.9)	40		0		2.7 ± 0.1	(1.2–6.2)	164
Total	5.5 ± 0.1	(1.9–11.4)	724	5.2 ± 0.1	(1.6–8.2)	108	3.0 ± 0.0	(0.8–9.2)	917

*Mean (mm) ± 1 standard error (range), N.

TABLE 6.

Mean heights for each of three morphological stages of *Diplothyra smithii* removed from dead shells monthly, January–August 1976.
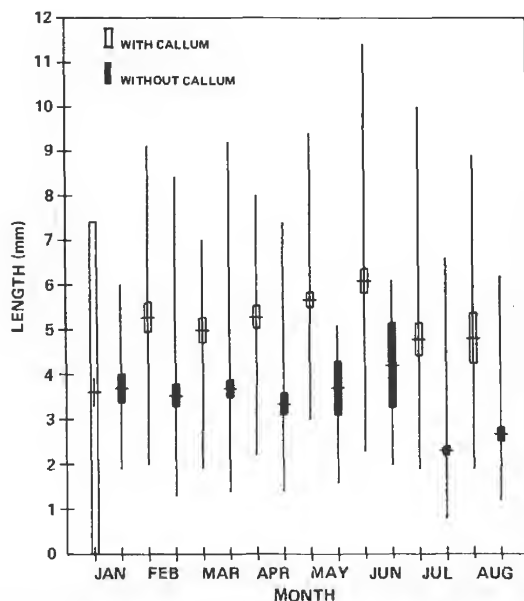
Month	With Callum			With Partial Callum			Without Callum		
January	2.4 ± 0.0	$(2.4-2.4)$	2^*		0		2.6 ± 0.1	$(1.4-4.3)$	50
February	3.6 ± 0.1	$(1.4-6.0)$	66	4.0 ± 0.1	$(1.9-6.2)$	56	2.6 ± 0.1	$(1.0-5.2)$	110
March	3.2 ± 0.1	$(1.4-4.8)$	62	2.9 ± 0.2	$(2.0-3.9)$	11	2.7 ± 0.1	$(1.2-6.3)$	154
April	3.3 ± 0.1	$(1.6-6.3)$	103	3.2 ± 0.1	$(1.1-4.4)$	40	2.5 ± 0.1	$(1.4-5.6)$	99
May	3.7 ± 0.1	$(1.7-6.5)$	221		0		2.9 ± 0.2	$(1.2-4.4)$	16
June	3.8 ± 0.1	$(1.4-6.8)$	160		0		3.0 ± 0.3	$(1.3-4.8)$	10
July	3.1 ± 0.1	$(1.3-6.2)$	70	3.7 ± 0.0	$(3.7-3.7)$	1	1.8 ± 0.0	$(0.7-4.0)$	314
August	3.0 ± 0.2	$(1.3-5.6)$	40		0		2.1 ± 0.0	$(0.9-4.6)$	164
Total	3.5 ± 0.0	$(1.3-6.8)$	724	3.6 ± 0.1	$(1.1-6.2)$	108	2.2 ± 0.0	$(0.7-6.3)$	917

*Mean (mm) $\pm$ 1 standard error (range), N.
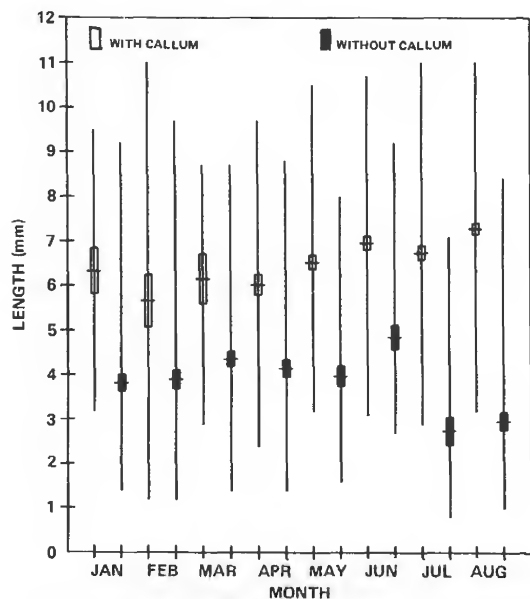
Figure 5. Mean length (horizontal line), one standard error of the mean (box), and size range (vertical line) of *D. smithii* with a callum (open box) and without a callum (solid box) removed from live shells: January–August 1976.

Figure 6. Mean length (horizontal line), one standard error of the mean (box), and size range (vertical line) of *D. smithii* with a callum (open box) and without a callum (solid box) removed from dead shells: January–August 1976.

are given in Tables 7 and 8. Female clams removed from live shells had significantly greater mean lengths and heights than females removed from dead shells.

Females removed from live shells had significantly greater mean lengths and heights when compared with mean lengths and heights of nonfemales of the same morphological stages (Table 7). There was a significant difference between the lengths of all females and nonfemales removed from dead shells (Table 8). Also there was a significant difference between the heights of females without a callum and nonfemales without a callum removed from dead shells;

however, there was no significant difference between the heights of females with a callum and nonfemales with a callum removed from dead shells (Table 8).

DISCUSSION

Oyster Shell Measurements

Oyster shells are the primary substratum for *D. smithii* in Mississippi Sound. Several characteristics of oyster shells, including the nature of the shell material (living or dead), the surface area available for setting, and the age and
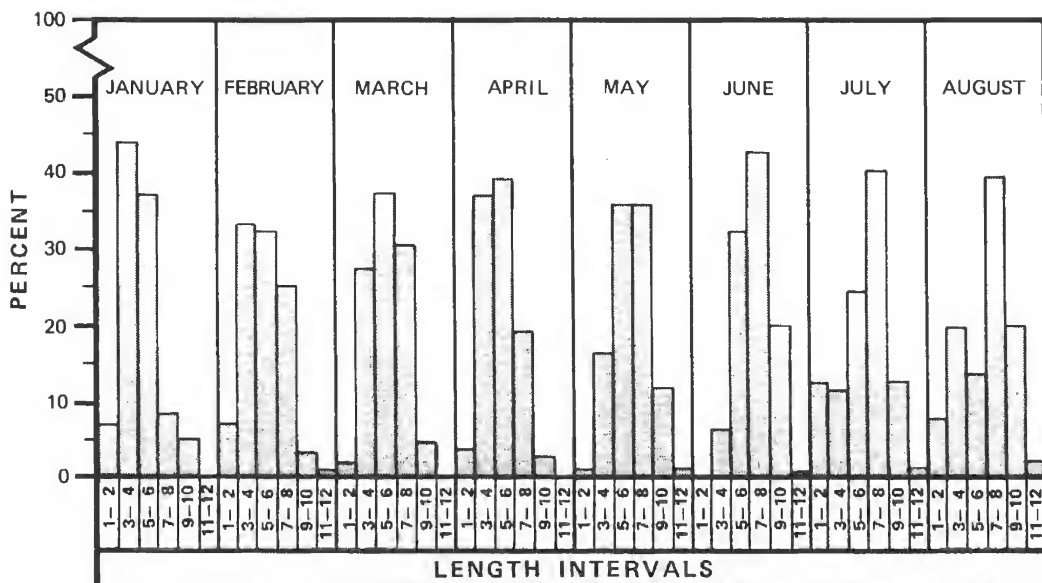
Figure 7. Length-frequency histograms for the composition of monthly samples of the population of *D. smithii* removed from live shells at Pass Marianne Reef.
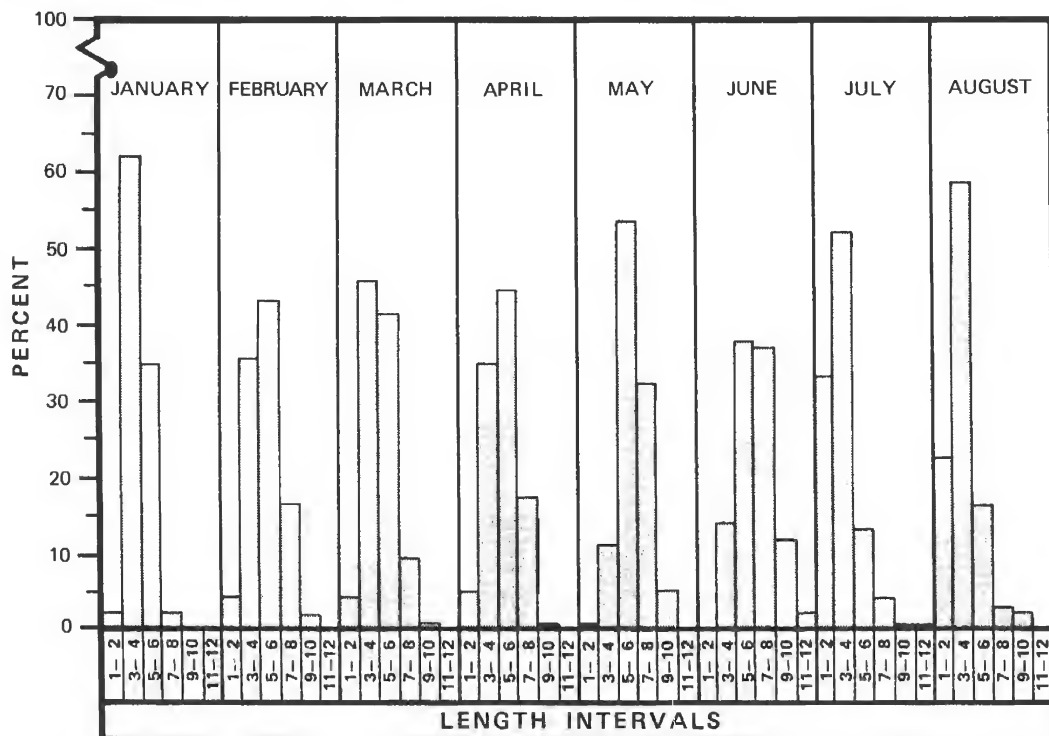

Figure 8. Length-frequency histograms for the composition of monthly samples of the population of *D. smithii* removed from dead shells at Pass Marianne Reef.

TABLE 7.

Comparison of lengths (A) and heights (B) of ovigerous female clams with and without a callum, and nonfemale clams with and without a callum, from live shells.

Month	Ovigerous Females		Nonfemale	
	With Callum	Without Callum	With Callum	Without Callum
	LENGTH (A)			
April	6.4 ± 0.3 (4.9 – 7.5) 11*	0	6.0 ± 0.1 (2.4 – 9.7) 139	4.1 ± 0.1 (1.4 – 8.8) 210
July	7.0 ± 0.2 (4.3 – 10.9) 56	0	6.7 ± 0.1 (2.9 – 11.0) 220	2.7 ± 0.2 (0.8 – 7.1) 103
August	7.3 ± 0.1 (3.2 – 10.6) 161	4.7 ± 0.4 (2.1 – 8.4) 15	7.2 ± 0.1 (3.6 – 11.0) 262	2.8 ± 0.1 (1.0 – 7.9) 179
Total	7.2 ± 0.1 (3.2 – 10.9) 228	4.7 ± 0.4 (2.1 – 8.4) 15	6.7 ± 0.1 (2.4 – 11.0) 621	3.4 ± 0.1 (0.8 – 8.8) 492
	HEIGHT (B)			
April	4.2 ± 0.2 (3.4 – 5.2) 11	0	4.0 ± 0.1 (1.6 – 6.6) 139	3.1 ± 0.1 (1.2 – 7.8) 210
July	4.5 ± 0.1 (2.3 – 7.3) 56	0	4.3 ± 0.1 (1.9 – 6.4) 220	2.1 ± 0.1 (0.5 – 5.0) 103
August	4.8 ± 0.1 (2.1 – 6.7) 161	3.5 ± 0.3 (1.4 – 6.2) 15	4.7 ± 0.0 (2.3 – 7.6) 262	2.2 ± 0.1 (1.0 – 6.3) 179
Total	4.7 ± 0.1 (2.1 – 7.3) 228	3.5 ± 0.3 (1.4 – 6.2) 15	4.4 ± 0.0 (1.6 – 7.6) 621	2.6 ± 0.0 (0.5 – 7.8) 492

*Mean (mm) ± 1 standard error (range), N.

TABLE 8.

Comparison of lengths (A) and heights (B) of ovigerous female clams with and without a callum, and nonfemale clams with and without a callum, from dead shells.

Month	Ovigerous Females		Nonfemale	
	With Callum	Without Callum	With Callum	Without Callum
	LENGTH (A)			
March	5.5 ± 0.9 (4.6 – 6.4) 2*	0	5.0 ± 1.4 (1.9 – 7.0) 60	3.7 ± 0.1 (1.4 – 9.2) 154
April	5.6 ± 0.2 (3.6 – 8.0) 35	5.6 ± 0.0 (5.6 – 5.6) 1	5.1 ± 0.2 (2.2 – 7.8) 68	3.3 ± 0.1 (1.4 – 7.4) 98
May	5.8 ± 0.1 (2.0 – 5.8) 93	0	5.9 ± 0.1 (3.0 – 9.4) 128	3.7 ± 0.3 (1.6 – 5.1) 16
July	4.9 ± 0.3 (1.9 – 10.0) 33	3.1 ± 0.1 (1.9 – 4.6) 46	4.7 ± 0.2 (2.4 – 7.8) 37	2.1 ± 0.0 (0.8 – 6.6) 268
August	4.4 ± 0.4 (2.1 – 8.2) 15	4.4 ± 0.2 (3.4 – 5.5) 9	5.1 ± 0.4 (1.9 – 8.9) 25	2.6 ± 0.1 (1.2 – 6.2) 155
Total	5.5 ± 0.1 (1.9 – 10.0) 178	3.4 ± 0.1 (1.9 – 5.6) 56	5.2 ± 0.1 (1.9 – 9.4) 318	2.8 ± 0.0 (0.8 – 9.2) 691
	HEIGHT (B)			
March	3.2 ± 1.0 (2.3 – 4.2) 2	0	3.2 ± 0.1 (1.4 – 4.8) 60	2.7 ± 0.1 (1.2 – 6.3) 154
April	3.4 ± 0.1 (2.0 – 4.5) 35	4.0 ± 0.0 (4.0 – 4.0) 1	3.3 ± 0.1 (1.6 – 6.3) 68	2.5 ± 0.1 (1.4 – 5.6) 98
May	3.8 ± 0.1 (2.0 – 5.8) 93	0	3.7 ± 0.1 (1.7 – 6.5) 128	2.9 ± 0.2 (1.2 – 4.4) 16
July	3.1 ± 0.2 (1.3 – 6.2) 33	2.4 ± 0.1 (1.2 – 4.0) 46	3.0 ± 0.1 (1.5 – 5.6) 37	1.7 ± 0.0 (0.7 – 3.2) 268
August	2.8 ± 0.2 (1.4 – 4.6) 15	3.3 ± 0.2 (2.7 – 4.2) 9	3.2 ± 0.2 (1.3 – 5.6) 25	2.0 ± 0.0 (0.9 – 4.6) 155
Total	3.5 ± 0.1 (1.3 – 6.2) 178	2.6 ± 0.1 (1.2 – 4.2) 56	3.4 ± 0.0 (1.3 – 6.5) 318	2.1 ± 0.0 (0.7 – 6.3) 691

*Mean (mm) ± 1 standard error (range), N.

thickness of specific shell regions may affect setting, density of infestation, growth rates, and morphological development of *D. smithii.*

Oyster thickness had the greatest effect on clam size and morphological maturity (see discussion on *Morphological Stages and Sizes*). Live shells had regions of greater thickness than dead shells. Dead shells varied less in overall thickness because of wear at both the umbo and ventral edges. Shell thickness may be related to the presence of burrowing organisms. Gunter (1953) suggested that the oyster may secrete additional shell material as a response to burrowing organisms. Thick shells may be an adaptive feature which prevents penetration by burrowers.

Percentage of Shells Infested

At Pass Marianne Reef, 71% of the live shells were infested with *D. smithii.* The prevalence of infestation in live shells could lead the reader to draw misleading conclusions. Prevalence of infestation does not indicate a preference of clams for live shells, rather it reflects the unsuitability of

dead shells for either initial or continued infestation. Whereas live oysters must be at least partially exposed, dead shells may be either exposed or buried, a factor which would affect initial infestation. Infested shells could be buried by dredge activities which would kill burrowing clams. Constant movement of the substratum by wave action also may prevent otherwise suitable dead shells from becoming infested (Gunter 1979).

The prevalence of infestation of live shells in this study (Table 1) was consistent with high values reported for the northern coast of the Gulf of Mexico (Galtsoff et al. 1935, Federighi and Collier [unpublished] cited by Hopkins 1949). Varying conditions affect the population of oysters present from year to year, as well as the numbers of burrowing clams. During the same time that the prevalence of *D. smithii* infestation increased on Pass Marianne Reef (1976–1978), the number of live oysters declined (Table 1). If fewer numbers of oysters were available for setting, a higher percentage may have been infested by the burrowing clam.

Density of Diplothyra smithii

Density of *D. smithii* was influenced by shell area and thickness, i.e., age of the oyster. The number of clams increased with an increase in shell area for both live and dead oysters (Figures 1 and 2). More clams were found in the dorsal quadrants of live shells than in other regions. Hofstetter (R. P. Hofstetter, Texas Parks and Wildlife Department, personal communication) also noted that heavy concentrations of clams were more common near the hinge (dorsal portion). This is the oldest region of the oyster and

thus has been available for setting clams longer than other parts. Danglade (1917) noted that burrowing clams were present primarily in larger and older shells. Densities of burrowing clams per oyster shell reported in this study are lower than those reported in previous studies (Higgins 1940, Collier [unpublished] cited by Hopkins 1949, Menzel 1950, Galtsoff 1964).

Morphological Stages of Diplothyra smithii

The proportion of burrowing clams in each morphological stage followed an annual pattern consistent with seasonal changes in water temperature. Undoubtedly water temperatures affected the rates of growth and burrowing, and the rate at which substratum limits were reached, at which time metamorphosis occurred and growth stopped. Seasonal changes in morphological stages are shown in Figures 3 and 4, and temperature and salinity changes are recorded in Figure 9. Clams spawned during the summer or fall of 1975 were predominantly immature during the first four months of 1976. Clams remained immature during the months when water temperatures were below 15°C.

Clams were found in the transition stage with partial callums from February through April. The presence of a partial callum indicated changes in morphological stage. These changes were most pronounced when water temperatures increased in March and April.

In May and June, callums had developed in most clams. Along with increased water temperatures, the ratio of immature to mature clams changed dramatically during May when the majority of clams from the 1975 spawning season
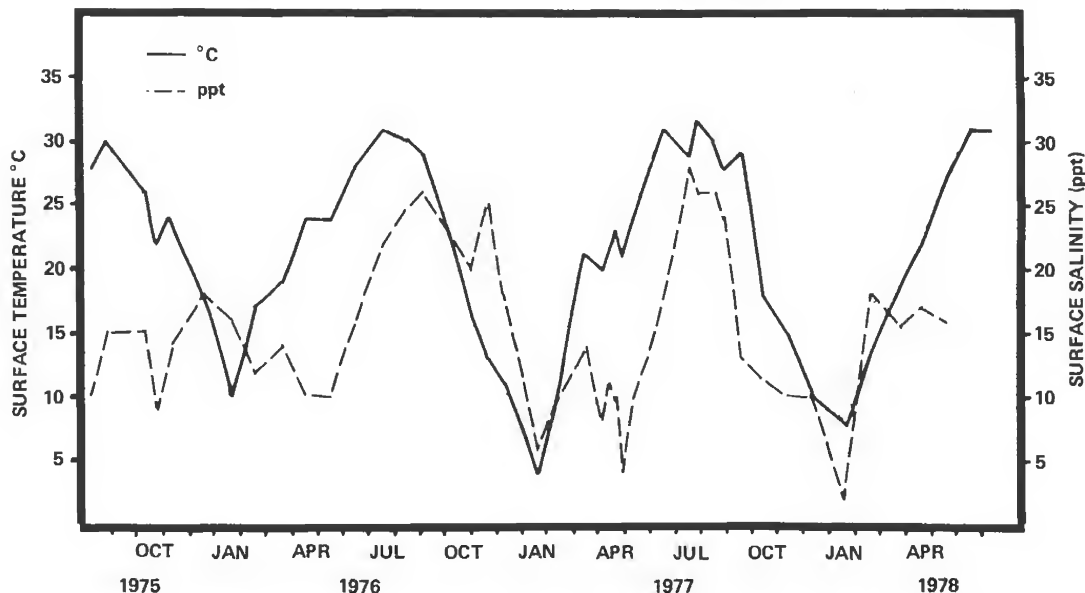

Figure 9. Surface salinity and temperature measurements from Pass Marianne Reef, August 1975 through July 1978.

reached substratum limits, metamorphosed, and matured. In July and August, recruitment of juvenile clams resulted in increased numbers of immature clams in dead shells. In live oysters the ratio of immature clams to mature clams remained approximately the same throughout the summer.

Although there were no differences between mean densities for live and dead oysters, there were differences in morphological maturation. Clams in thinner, dead shells reached the substratum limits faster than clams in live shells, and metamorphosed at smaller sizes (Tables 3 and 5). The larger percentage of mature clams observed in dead shells throughout 1976 may be related to the thinner valves of dead oysters.

Prior to this study, the attainment of a critical size (Evans 1968), crowding (Turner 1954), and substratum thickness (Smith 1969) were the only agents known to influence the production of a callum in the subfamily Martesiinae. This study indicated that, in addition to those factors, metamorphosis in *D. smithii* is induced also by seasonal temperature changes either directly or indirectly. There was a yearly cycle during which clams set in the summer or early fall and reached morphological maturity during the following spring and summer.

Sizes of Diplothyra smithii

Since growth ceases at metamorphosis (Turner 1954), factors which affect the onset of metamorphosis directly influence the size reached by *D. smithii*. Hence, mature clams vary in size depending on the thickness of the shell substratum which affects the onset of metamorphosis, and on environmental conditions which affect the rate of growth.

The mean lengths of mature clams removed from live and dead shells in this study were below the values reported by Tryon (1862), Turner (1955), Abbott (1974), and Andrews (1977). Although the largest clam from this study was comparable with that reported by Turner (1955), mature clams from Mississippi Sound were shorter than those reported in the literature. The umbonal-ventral sulcus dimensions recorded in this study were not comparable to the height measurements of previous investigators.

Although the clam may be oriented in the oyster shell at almost any angle, the majority of clams burrowed approximately perpendicular to the shell surface. The mean length of mature clams from live oysters (6.8 mm) can be related to the greater shell thickness at the dorsal margin (8.8 mm). The mean length of clams removed from dead shells (5.5 mm) also can be related to the thickness of those shells (5.7 mm).

Mean sizes from each month for clams from both live and dead shells (Figures 5 and 6) can be related to the monthly percentage of clams in given morphological stages (Figures 3 and 4). The size increase for clams with a callum, which began in March in dead shells (Figure 6) and in April in live shells (Figure 5), and continued through June, is not an indication for growth of mature clams. A callum indicates

that a clam is mature, and has terminated growth (Turner 1954). The increase in size resulted from the larger-sized, immature clams undergoing metamorphosis. The results in Figures 3 and 4 indicate that the number of mature clams increased slightly in April, then sharply in May and June. The change in size of mature clams during the same period (Figures 5 and 6) has been related to the maturation of immature clams.

The mean size of immature clams remained fairly constant from January through May, as larger, immature clams metamorphosed into mature clams. In July and August, decreases in mean length of immature clams resulted from summer spawning and the subsequent recruitment of small, postlarval clams in live and dead shells. Also in some dead shells, immature clams burrowed completely out of the shell, thus limiting both the number and size of immature and mature clams.

The length-frequency histograms (Figures 7 and 8) suggest a seasonal pattern of mid- to late-summer setting. From March through June, clams in smaller size classes from both shell types gradually decreased in number. With the onset of spawning in June, July, and August, numbers of clams in the 1- to 2-mm size class increased. In August, the numbers in the 3- to 4-mm size class increased, an indication of growth of clams which set during the months of June and July. Dead shells had a much lower frequency of clams in the larger size classes, particularly during July and August, probably related to shell thickness.

Sexually Mature Females

The size difference noted between females and nonfemales of *D. smithii* (Tables 7 and 8) may be evidence of sexual dimorphism. Among mollusks, particularly bivalves, sexual dimorphism is rarely obvious. Galtsoff (1964) found that in *Crassostrea virginica*, the sexual identity of the organism was influenced by size. He stated that oysters which were larger or were able to respond more quickly to favorable changes in the environment may develop into females first.

Several females from both shell types developed sexual maturity without a callum but developed only a small quantity of gonadal material. The presence of a completed callum was not a prerequisite for sexual maturity.

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Gulf Research Reports

Volume 7 | Issue 1

January 1981

A Preliminary Checklist of Marine Benthic Diatoms of Mississippi

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Recommended Citation

Sullivan, M. J. 1981. A Preliminary Checklist of Marine Benthic Diatoms of Mississippi. Gulf Research Reports 7 (1): 13-18.
Retrieved from http://aquila.usm.edu/gcr/vol7/iss1/2

A PRELIMINARY CHECKLIST OF MARINE BENTHIC
DIATOMS OF MISSISSIPPI

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ABSTRACT   A checklist of diatoms collected from various benthic habitats in coastal salt marshes and offshore seagrass beds of Mississippi has been compiled for the first time. The checklist includes 213 taxa (species and their varieties) in 43 genera with 19 of these taxa found only on the leaves of offshore seagrasses. *Synedra fasciculata* var. *intermedia* (Grun.) Sulliv. comb. nov. is proposed to be consistent with the nomenclature of the nominate variety. Future work with this ecologically important group of marine algae should result in many new additions to this preliminary checklist.

INTRODUCTION

The marine benthic diatom flora of Mississippi remained an unknown entity until the publications of Sullivan (1978, 1979a). This is somewhat surprising in view of the great ecological importance of these organisms as major constituents of the base of food webs in marine coastal ecosystems. Conger et al. (1972) compiled a list of diatoms from the Gulf of Mexico based on reviews of the older literature, and on results of phytoplankton collections in oceanic waters of the Gulf. Despite the broad coverage of their review, a great many species found in Mississippi by this author were not included in their checklist; an up-to-date list of diatoms in Mississippi's coastal environments was thought to be needed. Furthermore, the present checklist reflects current taxonomic thinking, and restricts itself to a specific component of the flora (i.e., those forms leading a benthic existence).

Other major groups of marine algae in Mississippi have fared little better than the diatoms and only two published studies could be found. Humm and Caylor (1957) surveyed the blue-green, green, red, and brown algae of Mississippi Sound during two consecutive summers. The majority of collections were made around Ship Island, although a few were noted from such localities as Deer Island and a salt marsh near Ocean Springs. Sage and Sullivan (1978) collected blue-green algae from Graveline Bay Marsh over a yearly cycle, and noted the similarity between their flora and those of Atlantic coastal salt marshes.

CHECKLIST COVERAGE

Although the geographical limits of the checklist theoretically include all benthic habitats of the Mississippi coast and its salt marshes, as well as those of Mississippi Sound and its offshore barrier islands, the number of localities sampled are few and the actual coverage represents a very small percentage of the total area just defined. However, the similarity of the diatom flora from different salt marshes or seagrass beds suggests that the checklist, although pre-

liminary, is representative of the character of the marine benthic diatom flora of Mississippi. This similarity also suggests that the number of additions to the checklist will decrease with each new locality sampled.

The present checklist is biased towards the edaphic (sediment-associated) diatom flora of coastal salt marshes. Most of this work has been conducted in Graveline Bay Marsh which is located ca. 11 km southeast of the Gulf Coast Research Laboratory, Ocean Springs, Mississippi. Some of this work has been published (Sullivan 1978); the remaining data have been submitted for publication but without a complete listing of all diatom species encountered. Three different salt marshes in St. Louis Bay, MS, have been sampled, and these unpublished data also have been incorporated into this checklist. In addition, diatoms epiphytic on the red algae *Caloglossa leprieurii* (Mont.) J. Ag. and *Bostrychia radicans* Mont. in St. Louis Bay also have been included. Three different seagrass species in beds off the north shore of Horn Island recently were sampled (Sullivan 1979a) and form an important part of the checklist. Therefore, the flora reported herein is of an edaphic or epiphytic nature, and represents both inshore and offshore habitats.

CHECKLIST FORMAT

For the purposes of this checklist, diatoms are considered to constitute the single class Bacillariophyceae. There is no universal agreement among authorities as to which division diatoms should be assigned, and there is even less agreement on the number and identity of orders and families that should be recognized. Hendey (1974) provides pertinent comments on the problems involved in arriving at a natural classification of diatoms, and reviews the different classification systems that have been proposed. The most recently proposed classification is that of Simonsen (1979) who recognizes two orders, five suborders, and 21 families. In view of the flux and uncertainty characterizing current thinking concerning relationships between higher taxonomic categories, the present checklist is concerned only with genera and species of Bacillariophyceae in marine benthic habitats of Mississippi. Genera are arranged alphabetically, and species

and their varieties are arranged alphabetically within each genus following the format of Hendey's (1974) checklist of British marine diatoms. Numbers in brackets after a name refer to **NOTES** which immediately follow the checklist. Species and their varieties collected only from offshore seagrass beds are marked with an asterisk.

BACILLARIOPHYCEAE

ACHNANTHES Bory, 1822
    biasolettiana var. *sublinearis* Grun.
    brevipes var. *intermedia* (Kütz.) Cl.
    coarctata (Bréb.) Grun.
    curvirostrum Brun
    hauckiana Grun.
    lanceolata var. *dubia* Grun. (15)
    lemmermanni Hust.
    temperei M. Perag.
AMPHIPRORA Ehrenberg, 1843
    gigantea var. *decussata* (Grun.) Cl.
    hyalina Eulenstein
    paludosa W. Sm.
        var. *paludosa*
        var. *duplex* (Donk.) V.H.
    pulchra Bailey
    similis Hust.
AMPHORA Ehrenberg, 1831
    angusta Greg.
        var. *angusta* (1)
        var. *oblongella* Grun.
    caroliniana Giffen (2)
    coffeiformis (Ag.) Kütz.
    cymbelloides Grun.*
    cymbiformis Cl.*
    exigua Greg.
    laevis var. *perminuta* Grun.
    libyca Ehr.
    pediculus (Kütz.) Grun.*
    proteus Greg.
    robusta Greg.*
    sabyii Salah
    tenerrima Hust.
    tenuissima Hust.
ANAULUS Ehrenberg, 1844
    balticus Simonsen
ANOMOEONEIS Pfitzer, 1871
    vitrea (Grun.) Ross (3)
BACILLARIA Gmelin, 1778
    paxillifer (Müll.) Hendey (4)
BERKELEYA Greville, 1827
    rutilans (Trent.) Grun. (5)
CALONEIS Cleve, 1894
    westii (W.Sm.) Hendey
CAMPYLOSIRA Grunow, 1882
    alexandrica Salah
    cymbelliformis (A.S.) Grun.
CAPARTOGRAMMA Kufferath, 1956
    crucicula (Grun.) Ross

COCCONEIS Ehrenberg, 1838
    deperdita Giffen
    cf. *discrepans* A.S.
    disculoides Hust.
    placentula var. *euglypta* (Ehr.) Grun.
    placentula var. *lineata* (Ehr.) V.H.
    scutellum Ehr.
        var. *scutellum*
        var. *parva* (Grun.) Cl.
    woodii Reyes-Vasquez* (6)
CYCLOTELLA Kützing, 1833
    caspia Grun.
    meneghiniana Kütz.
    stylorum Brightwell
CYLINDROTHECA Rabenhorst, 1859
    gracilis (Bréb.) Grun.
CYMATOSIRA Grunow, 1862
    belgica Grun.
CYMBELLA Agardh, 1830
    pusilla Grun. (7)
DENTICULA Kützing, 1844
    subtilis Grun.
DIMEREGRAMMA Ralfs, 1861
    hyalinum Hust.
    minor (Greg.) Ralfs
DIPLONEIS Ehrenberg, 1840
    aestuari Hust.
    elliptica (Kütz.) Cl.
    gruendleri (A.S.) Cl.
    mediterranea (Grun.) Cl.
    obliqua (Brun) Hust.*
    pseudovalis Hust.
    puella (Schum.) Cl.
    smithii (Bréb.) Cl.
EUNOTIA Ehrenberg, 1837
    naegelii Migula (8)
EUNOTOGRAMMA Weisse, 1854
    laevis (*laeve*) Grun.
FRAGILARIA Lyngbye, 1819
    atomus Hust.
    gessneri Hust.
    hyalina (Kütz.) Grun.*
    obtusa Hust.
    pinnata Ehr.
    schulzi Brockmann
FRUSTULIA Agardh, 1824
    asymmetrica (Cl.) Hust.
    rhomboides var. *saxonica* (Rabh.) DeToni
    similis Hust.

GRAMMATOPHORA Ehrenberg, 1840
  oceanica Ehr.*
GYROSIGMA Hassall, 1845
  balticum (Ehr.) Rabh.
  beaufortianum Hust.
  macrum (W.Sm.) Griff. & Henfr.
  obliquum (Grun.) Boyer
  obscurum (W.Sm.) Griff. & Henfr.
  peisonis (Grun.) Hust.
HANTZSCHIA Grunow, 1880
  distincte-punctata Hust.
LICMOPHORA Agardh, 1827
  abbreviata Ag.*
  cf. *debilis* (Kütz.) Grun.*
MASTOGLOIA Thwaites, 1856
  exigua Lewis
  pumila (Grun.) Cl.
  pusilla Grun.*
MELOSIRA Agardh, 1824
  dubia Kütz.
  lineata (Dillw.) Ag.
  moniliformis (Müll.) Ag.
  nummuloides Ag.
  westii W.Sm.
NAVICULA Bory, 1822
  abunda Hust.
  accomoda Hust.
  aequorea Hust.
  alpha Cl.
  ammophila Grun.
  amphipleuroides Hust.*
  binodulosa Sulliv. & Reim. (9)
  capitata var. *hungarica* (Grun.) Ross
  circumtexta Meister
  clamans Hust.
  clementis Grun.
  cocconeiformis Greg.
  creuzburgensis Krasske
  digito-radiata (Greg.) Ralfs
  diserta Hust.
  fauta Hust. (10)
  fenestrella Hust.
  flanatica Grun.
  florinae Møller
  gregaria Donkin
  hanseni Møller
  hudsonis Grun. (11)
  incerta Grun.
  incomposita Hagelstein
  longirostris Hust.
  maculata (Bailey) Edwards
  mendotia VanLand.
  cf. *menisculus* Schum.
  mutica Kütz. (12)
  nolens Simonsen

obsoleta Hust.
orbiculata Patrick (13)
pavillardi Hust.*
peregrina (Ehr.) Kütz.
phyllepta Kütz.
pseudocrassirostris Hust.
pseudony Hust.
pusilla W.Sm.
radiostriata Hust.
regularis Hust.
rhynchocephala Kütz.
salinarum Grun. (14)
salinicola Hust. (15)
schroeteri Meister
spicula (Hickie) Cl.
subforcipata Hust.
subirritans Giffen
taraxa Hohn & Hellerm. (16)
tenera Hust.
teneroides Hust.
tripunctata (Müll.) Bory (15,17)
yarrensis Grun.
zostereti Grun.
NITZSCHIA Hassall, 1845 (18)
  angularis W.Sm.
  apiculata (Greg.) Grun.
  bilobata var. *ambigua* Manguin
  brevissima Grun. (19)
  calida Grun.
  closterium (Ehr.) W.Sm.
  communis var. *hyalina* Lund
  constricta (Greg.) Grun.*
  dissipata (Kütz.) Grun.
  dubia W.Sm.
  dubiformis Hust.
  epithemoides Grun.
  fasciculata (Grun.) Grun.
  filiformis (W.Sm.) Schütt
  gandersheimiensis Krasske (20)
  grana Hohn & Hellerm.
  granulata Grun.
  hungarica Grun.
  hustedtiana Salah
  levidensis (W.Sm.) V.H.
  lorenziana Grun.
    var. *lorenziana*
    var. *subtilis* Grun.
  microcephala Grun.
  minutula Grun. (15,21)
  obsidialis Hust.
  obtusa W.Sm.
    var. *obtusa*
    var. *nana* Grun. (15)
  palea (Kütz.) W.Sm.
  paleacea Grun.*

panduriformis Greg.
    var. *panduriformis*
    var. *continua* Grun.
perversa Grun.
plana W.Sm.
pseudoamphioxys Hust. (22)
recta Hantz.
romana Grun.
romanoides Manguin
scalaris (Ehr.) W.Sm.
sigma (Kütz.) W.Sm.
socialis var. *massiliensis* Grun.
subvitrea Hust.
tryblionella Hantz.
visurgis Hust.
vitrea var. *salinarum* Grun.
OPEPHORA Petit, 1888
  pacifica (Grun.) Petit
  parva (Grun.) Krasske
  schwarzii (Grun.) Petit
PARALIA Heiberg, 1863
  sulcata (Ehr.) Cl. (23)
PLAGIOGRAMMA Greville, 1859
  tenuistriatum Cl.
PLEUROSIGMA W. Smith, 1852
  delicatulum W.Sm.
  distinguendum Hust.
  salinarum (Grun.) Grun.

strigosum W.Sm.
RHOPALODIA O. Müller, 1895
  gibberula (Ehr.) Müll.
STAURONEIS Ehrenberg, 1843
  amphioxys Greg.
    var. *amphioxys*
    var. *obtusa* Hendey
  salina W.Sm.
STRIATELLA Agardh, 1832
  unipunctata (Lyngbye) Ag.*
SURIRELLA Turpin, 1828
  atomus Hust.
  litoralis Hust.
  ovalis Bréb.
  striatula Turpin
SYNEDRA Ehrenberg, 1830
  fasciculata (Ag.) Kütz. (24)
    var. *fasciculata*
    var. *intermedia* (Grun.) Sulliv. *comb. nov.** (24)
THALASSIOSIRA Cleve, 1873
  eccentrica (Ehr.) Cl. (25)
TRACHYNEIS Cleve, 1894
  aspera (Ehr.) Cl.*
TRACHYSPHENIA Petit, 1877
  acuminata Perag.*
TROPIDONEIS Cleve, 1891
  lepidoptera (Greg.) Cl.
  vitrea (W.Sm.) Cl.

NOTES

(1) See Hendey (1974) for differences between *A. angusta* and *A. ventricosa* Greg.

(2) Giffen (1980) examined the type slide of *Amphora granulata* Greg. and concluded that *A. granulata* sensu Hustedt (1955) represented a previously undescribed taxon, which he named and described as *A. caroliniana* after the type locality.

(3) Only two valves were found in a St. Louis Bay salt marsh.

(4) This taxon is better known as *Bacillaria paradoxa* Gmelin, but the correct name is *B. paxillifer* if one recognizes the validity of the genus *Bacillaria*. The former specific epithet aptly describes the paradoxical movements of colonial associations of this organism which have fascinated botanists for almost 200 years.

(5) See Cox (1975a,b) for the separation of the genera *Berkelya* and *Amphipleura* Kützing.

(6) *Cocconeis woodii* differs from *C. scutellum* only by its sigmoid axial area on both valves of the frustule, and perhaps deserves only a varietal rank. In any event, the two entities clearly were separable in collections of epiphytic seagrass diatoms.

(7) *Cymbella pusilla* is perhaps the only true marine member of the genus.

(8) Only three valves were found in a St. Louis Bay salt marsh.

(9) This taxon originally was described from a Delaware salt marsh by Sullivan and Reimer (1975), and only has been found within the sediments beneath *Distichlis spicata* (L.) Greene in Mississippi salt marshes.

(10) *Navicula fauta* was first described by Hustedt (1954) from mangrove vegetation on the Pacific Coast of El Salvador, and has not been reported since to the best of my knowledge.

(11) Considered to be conspecific with the earlier described taxon *N. pygmaea* Kütz. by Simonsen (1975).

(12) Includes *N. mutica* var. *cohnii* (Hilse) Grun. as described by Patrick and Reimer (1966).

(13) Observed only once in Graveline Bay Marsh.

(14) Includes f. *minima* Kolbe which is likely to be identified by some authorities as *N. cryptocephala* var. *veneta* (Kütz.) Rabh.

(15) One of the most abundant and characteristic salt marsh diatom taxa.

(16) May be a synonym for *N. platyventris* Meister described earlier.

(17) Later synonyms are *N. transversa* Bory and *N. gracilis* Ehr. (Patrick and Reimer 1966). See Cox (1979) for a detailed study of this highly variable and widely distributed taxon.

(18) The revisions of Lange-Bertalot (1976), and Lange-Bertalot and Simonsen (1978) were used in identifying taxa belonging to the section Lanceolatae.

(19) This taxon is identical with *Nitzschia parvula* Lewis.

(20) Most specimens identified as this taxon fit the description of *Nitz. laevis* Hust., which is very likely a synonym of *Nitz. gandersheimiensis* according to Lange-Bertalot and Simonsen (1978).

(21) Those individuals identified as *Nitzschia frustulum* (Kütz.) Grun. in Sullivan (1978) belong to this taxon based on interpretations of Lange-Bertalot (1976).

(22) A very abundant diatom of Graveline Bay Marsh that could be mistaken for *Hantzschia amphioxys* var. *minor* Perag.

(23) See Crawford (1979) for an excellent description of this taxon and its separation from *Melosira*.

(24) Patrick and Reimer (1966) have determined that *Synedra affinis* Kütz. and *S. tabulata* (Ag.) Kütz. are later synonyms of *S. fasciculata* (Ag.) Kütz. Therefore, *S. (affinis* var.) *intermedia* Grun. in Van Heurck is to be properly regarded as a variety of *fasciculata*. See Sullivan (1979b) for a description of var. *intermedia*.

(25) Based on the frequency of its appearance in salt marsh sediments, *Thalassiosira eccentrica* may be capable of a benthic as well as a planktonic existence.

GENERAL SUMMARY

A total of 213 taxa (species and their varieties) in 43 genera comprise the present checklist. Genera with the largest number of taxa are *Navicula* and *Nitzschia* with 53 and 44, respectively. This is not surprising in light of a sampling bias towards forms inhabiting salt marsh sediments where motility would appear to be a distinct advantage. The third most important genus in terms of number of taxa is *Amphora*, which also possesses a raphe system on both valves of the frustule (unicell). Also well represented are *Achnanthes*, *Cocconeis*, and *Diploneis* with eight taxa each.

Exactly 19 taxa were collected only from the leaves of offshore seagrasses in Mississippi Sound. If more collections were made in the seagrass beds, this number certainly would have been much higher. Clearly, the physicochemical characteristics of the waters that bathe diatom cells in inshore and offshore habitats are different as is evidenced by the distribution of diatom genera and taxa (e.g., *Grammatophora*, *Licmophora*, *Striatella*, and *Trachysphenia* are thus far only known from seagrass beds).

The present checklist provides important distributional information on an ecologically significant group of organisms. Future work along the Mississippi coast and in the Sound should result in many new additions to this preliminary checklist, and hopefully will encourage other workers in the remaining Gulf coastal states to compile similar checklists.

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January 1981

Larval Development Under Laboratory Conditions of the Xanthid Mud Crab *Eurytium limosum* (Say, 1818) (Brachyura: Xanthidae) from Georgia

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LARVAL DEVELOPMENT UNDER LABORATORY CONDITIONS OF THE XANTHID MUD CRAB *EURYTIUM LIMOSUM* (SAY, 1818) (BRACHYURA: XANTHIDAE) FROM GEORGIA

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ABSTRACT   Larvae of the xanthid mud crab *Eurytium limosum* were reared in the laboratory from hatching to first crab stage. Four zoeal stages and one megalops stage were obtained and are described. Complete larval development required about 15 days under culture conditions of 26.0° to 28.0°C and 25 ppt sea water. A long antenna and short antennal exopods consign *E. limosum* to the Group I xanthid zoeae of Rice (1980). The first stage zoea closely resembles that of *Panopeus herbstii* and is distinguished by having the dorsal spine strongly recurved at the extremity. Stages 2 to 4 are distinguished from *Rhithropanopeus harrisii* and *Neopanope sayi* larvae by having two lateral spines on the telson.

INTRODUCTION

Xanthid larvae have been the subject of more studies than have larvae of any other family within the Brachyura. Wear (1970) in his bibliography of xanthid crab larvae listed 23 references to xanthid larvae, exclusive of the 25 references given by Gurney (1942). More recently, Rice (1980) summarized current knowledge of xanthid larvae and listed 15 references not found in Wear (1970) or published since that time. Not listed by Rice (1980) were the descriptions of larvae belonging to *Pilumnoides perlatus* by Fagetti and Campodonico (1973), and to *Neopanope texana* by McMahan (1967). Since Rice's review, the larvae of *Micropanope barbadensis* have been described by Gore et al. (1981).

Xanthids generally are characterized by having four zoeal stages and a megalops stage, although five species have been shown to have less than four zoeal stages (Hale 1931; Wear 1967, 1968; Saba et al. 1978); the five exceptions are from somewhat restricted habitats. Members of the subfamily Menippinae have five and sometimes six zoeal stages, but there is strong evidence that these crabs constitute a separate family (Scotto 1979). Only one other xanthid crab, *Pilumnoides perlatus* (Poeppig, 1936), has been shown to have five zoeal stages (Fagetti and Campodonico 1973).

The xanthid genus *Eurytium* Stimpson, 1859 is represented in North America by three species, only one of which occurs on the eastern coast of North America (Rathbun 1930). Though primarily a tropical species associated with mangrove habitats, the mud crab *Eurytium limosum* (Say, 1818) is a common member of the *Spartina* salt marsh fauna of coastal Georgia and southern South Carolina (Teal 1959, Williams 1965), and it is probable that its larvae represent an important part of the estuarine meroplankton in those and other regions.

The present study is the first description of larvae within

the genus *Eurytium*, and is in part the result of studies conducted at Sapelo Island, Georgia, by Kurata (1970).

MATERIALS AND METHODS

An ovigerous female captured in a *Spartina* marsh adjacent to Sapelo Island, Georgia, on August 16, 1964, was kept at room temperature in a large finger bowl half filled with filtered sea water diluted to 25 ppt until August 21, 1964, when the eggs hatched. Most of the zoeae were placed in three large finger bowls. Later, the first stage zoeae were placed in 10 small 3.5-inch finger bowls in groups of 10 per bowl and maintained at 26.0° to 28.0°C in 25 ppt filtered sea water. Water in the finger bowls was changed daily, and a record was maintained of larval molting and mortality. All zoeal and megalops stages were fed once daily on newly hatched *Artemia* nauplii. Various stages used for the descriptions were removed from the large mass-culture bowls and fixed in 10% formalin; 48 hours later, stages were transferred to 70% ethanol. Drawings were made with the aid of Wild M-5 and M-20 drawing tubes; an ocular micrometer was used for all measurements. Preserved larval stages and the parent currently are in the collection of the senior author.

RESULTS

Rearing

Results of rearing experiments are summarized in Figure 1. Mortality of larvae was negligible during the zoeal stages, but was considerable in the megalops stage. Mean duration of each zoeal stage was 2 to 3 days and that of megalops was about 8 days. Complete larval development required from 8 to 15 days; molting to first crab stage occurred between days 16 and 19.

Larval Stages

Four zoeal stages (Figures 2 and 3) and one megalops stage (Figure 4A–C) are recognized. No additional zoeal stages were observed.
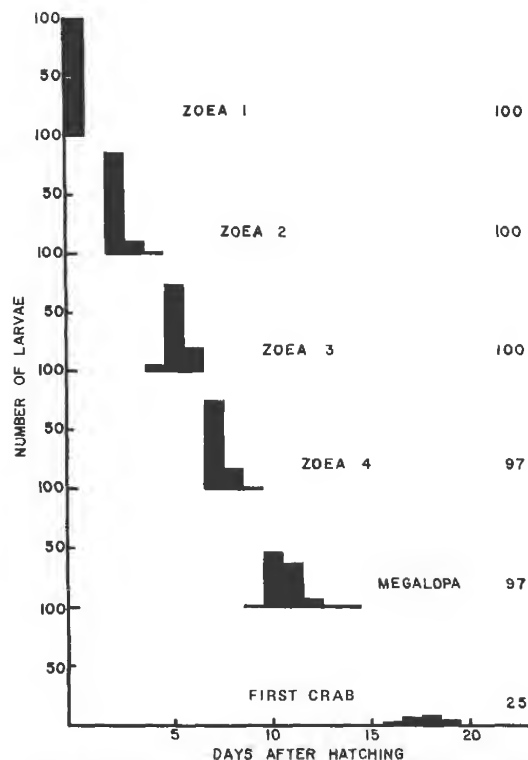
Figure 1. Duration and success of larval stages during development of *Eurytium limosum.* One hundred newly hatched zoeae were reared in 10 small finger bowls at 26.0° to 28.0°C, at 25 ppt. Figures on right hand side of diagram show the total number of larvae successfully reached at each stage.

Zoea

Carapace with 1 dorsal, 1 rostral, and 2 lateral spines. These are all smooth with the rostral spine long and almost straight. Dorsal spine about 3/4 the carapace length (measured from tip of rostral spine to posterior margin of carapace), curving posteriorly at the end. Lateral spines small, about 1/8 length of dorsal spine. Small anterior and posterior protuberances on carapace. Ventral margin of carapace smooth and fringed with up to 10 hairs, increasing in number with the progression of stages. Abdomen (measured from posterior of carapace to tip of telson forks) about 1.1 times longer than carapace, lateral hooks present on segments 2 and 3, those on segment 3 distinctly smaller than those on segment 2. A pair of lateral spines present on segments 3 to 5, these spines all nearly the same size and never reaching the posterior margin of the following segment.

Telson with 1 dorsal and 2 lateral spines, second lateral spine quite small, hairlike and seen only in the first stage. First lateral and dorsal spines distinct in all stages, though the former decreases in size in later stages. Telson forks

slender, smooth, and curving dorsally at end. Central indentation on posterior margin wide but shallow. Three pairs of internal spines, the third pair (innermost) longest and slightly longer than 1/2 the length of telson fork.

Antennae nearly equal to or slightly longer than rostral spine; exopod is vestigial and represented by a small process with a short terminal spine (sometimes wanting) at the base of the spinous process. Spinous process furnished distally with several spinules in stage 1, but smooth in later stages.

Stage 1 (Figures 2A, B; 3A, E). Carapace length: 1.13 mm. Eyes sessile. No ventral, marginal setae on carapace. Sixth abdominal segment fused with telson. Telson fork length nearly equal to width of telson (measured at the level of the first internal spine). Antennule represented by a simple conical process with single group of terminal aesthetes. No endopod on antenna, mandible with no palp. No outer setae on maxillule. First and second maxillipeds bear 4 swimming setae on each exopod. No third maxillipeds, pereopods, or abdominal appendages.

Stage 2 (Figures 2C; 3B, F). Carapace length: 1.43 mm. Eyes stalked and free from carapace. Base of rostral spine slightly expanded laterally just in front of eyes but not produced into distinct spines. Two hairs on inner ventral margin of carapace. Second lateral spine on telson disappears in this stage. Inconspicuous swelling at base of antennal spinous process representing rudimentary endopod. Densely plumose outer setae on maxillule. Six swimming setae on exopod of first maxilliped, 7 setae on exopod of second maxilliped. Third maxilliped and pereopods appear as small buds.

Stage 3 (Figures 2D; 3C, G). Carapace length: 1.90 mm. Sixth abdominal segment articulated from telson. A pair of small setae added between innermost pair of internal spines of telson. Length of telson forks about 1 1/4 times longer than width of telson. Endopod of antenna about 1/8 length of spinous process. First and second maxillipeds each bear 8 swimming setae on exopods. First pereopod bilobed. Pleopods appear as simple conical buds, those on segments 3 and 4 shorter than respective lateral spines of segments.

Stage 4 (Figures 2E-J; 3D, H). Carapace length: 2.17–2.43 mm. Telson usually with 2 pairs of small internal setae between innermost pair of spines. Antennule greatly swollen at base; outer flagellum segmented from protopod and bearing 3 groups of aesthetes, inner flagellum appears as a simple process. Mandible (Figure 2F) well calcified with incisor and molar processes distinctly divided, and with small palp. Endopod of maxillule (Figure 2G) consists of 2 segments with a seta on short proximal segment and 6 setae in 3 groups on long distal segment. A simple outer seta present near base of maxillule. Endopod of maxilla (Figure 2H) unsegmented but divided into 3 indistinct inner lobes with 3, 2, and 3 setae on each respective lobe. Endopod of first maxilliped has on terminal segment a vestigial, outer seta not reaching distal end of terminal segment (Figure 2I). Exopod of first maxilliped with 8 or 9 setae,
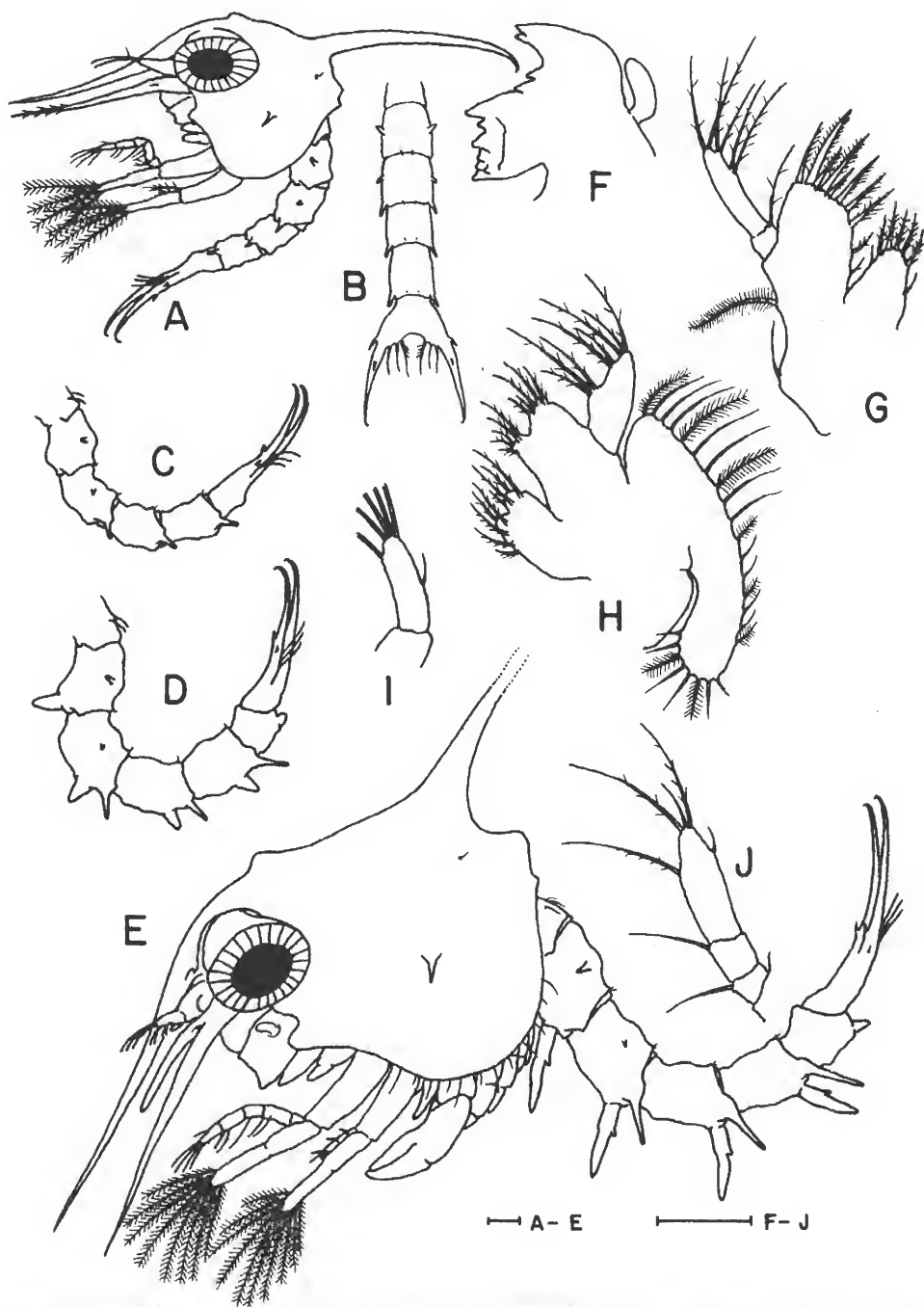
Figure 2. *Eurytium limosum*, zoeal stages 1 to 4. Stage 1 zoea: A, lateral view; B, dorsal view of abdomen. Stage 2 zoea: C, lateral view of abdomen. Stage 3 zoea: D, lateral view of abdomen. Stage 4 zoea: E, lateral view; F, mandible; G, maxillule; H, maxilla; I, terminal segment of maxilliped 1; J, endopod of maxilliped 2. (0.1 mm indicated.)

Figure 3. *Eurytium limosum*, zocal stages 1 to 4, A–D, dorsal view of telson: A, stage 1; B, stage 2; C, stage 3; D, stage 4. E–H, antenna: E, stage 1; F, stage 2; G, stage 3; H, stage 4. (0.1 mm indicated.)
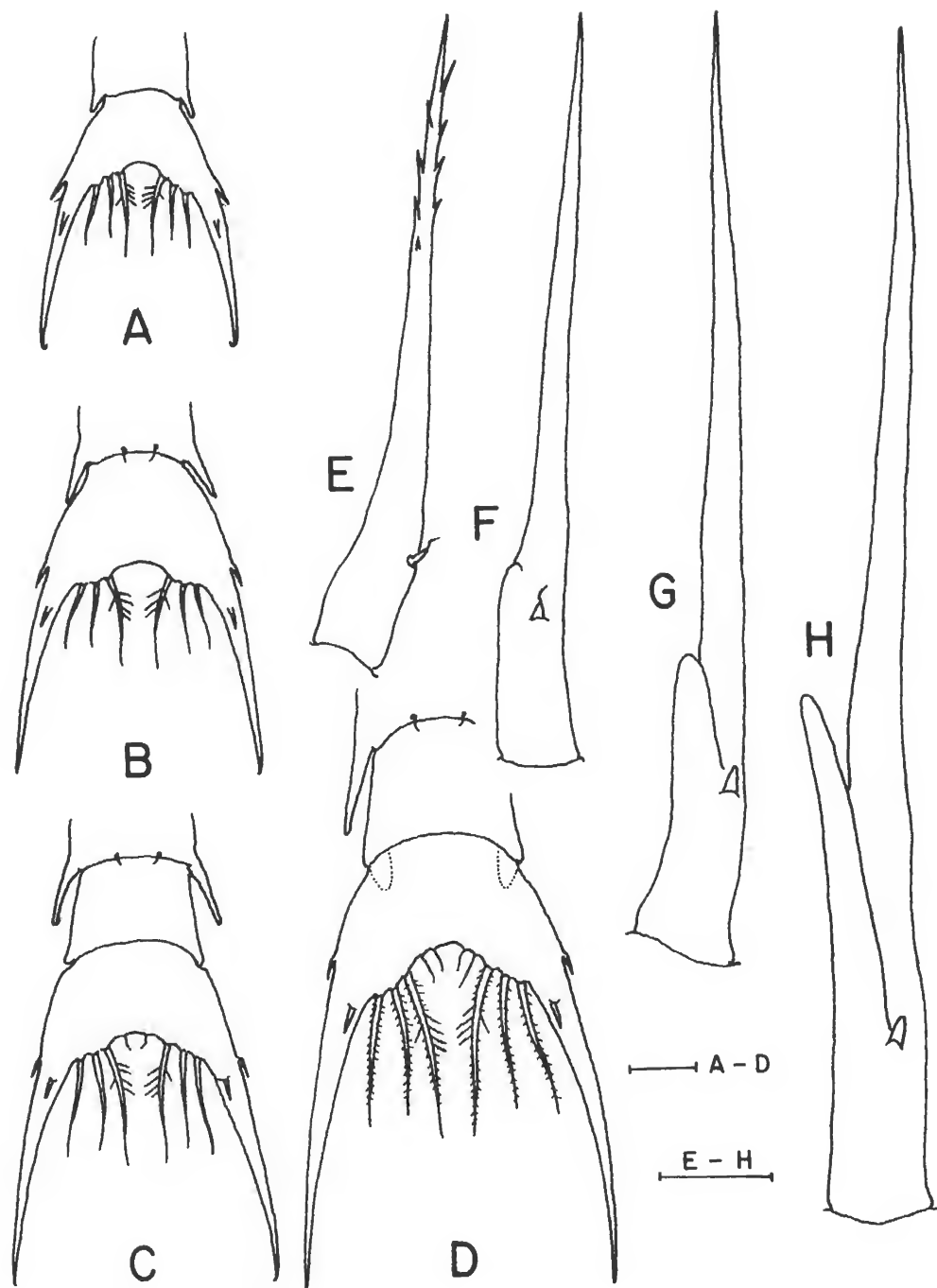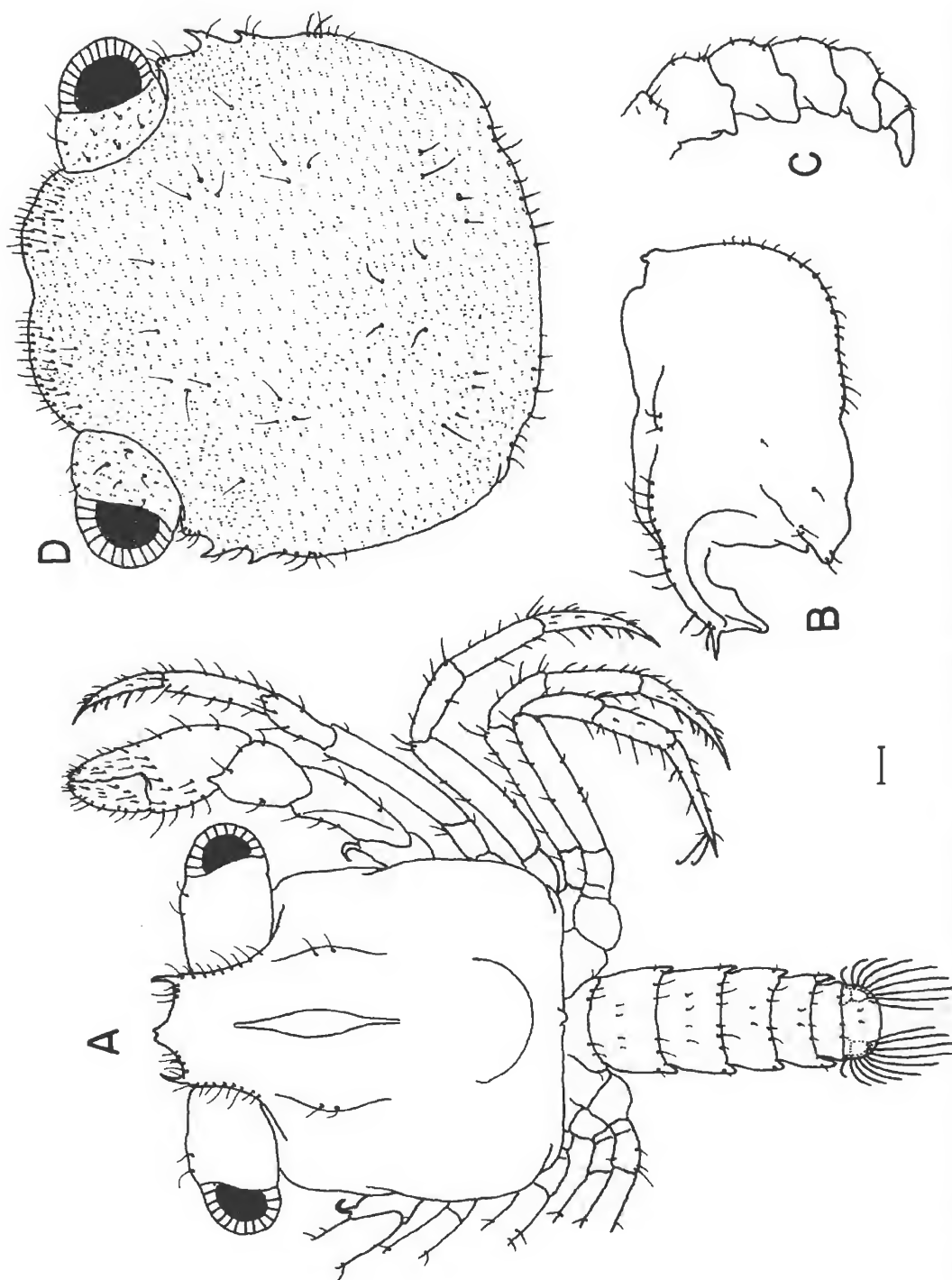
Figure 4. *Eurytium limosum*, megalopa and first crab. A–C, megalopa: A, dorsal view; B, lateral view of carapace; C, lateral view of abdomen. D, dorsal view of carapace of first crab stage. (0.1 mm indicated.)

Endopod of second maxilliped consists of 3 segments, the second slightly longer than the first, the third (terminal) segment about 1 1/2 times length of combined proximal 2 segments (Figure 2J). Proximal 2 segments bear 1 seta each, terminal segment bears 3 apical, 1 inner, and 1 outer setae. Exopod of second maxilliped with 10 or 11 setae. Pereopod buds exposed from ventral margin of carapace. Carapace fringed with up to 10 setae. Pleopods with rudimentary endopods, those on segments 3 and 4 longer than respective lateral spines.

Megalops (Figures 4A-C). Carapace length: 1.06 mm. Total length: 2.01 mm. Carapace slightly longer than wide, without conspicuous dorsal protuberances. Gastric and cardiac regions distended dorsally. Small process at center of posterior margin. Eyes extend somewhat beyond lateral margin of carapace; cornea not wider than stalk.

Rostrum bent obliquely down and terminates as slightly bifid, blunt central process with pair of pointed lateral spines that extend almost horizontally forward, curving inwardly like horns.

Abdomen slightly shorter than carapace. Lateral plate of segment 5 nearly reaching posterior end of segment 6. Telson about 2/3 as long as wide and slightly longer than segment 6, with rounded posterior margin. Uropod bears 1 seta on proximal segment (protopod) and 8 or 9 setae on distal segment (exopod).

Protopod of antenna with 4 segments and a flagellum of 7 segments. Mandible with 3-segmented palp. Cheliped with large curved hook on ischium. No other spines or hooks present on any pereopod segments, except dactyli of pereopods 2 to 4 which bear 3 short spines. Dactyli of pereopods 2 to 5 about 1 1/2 times longer than their propodi. Fifth pereopod bears 2 short aesthetasc-like hairs on dactyl.

First Crab (Figure 4D). Carapace length: 1.33 mm. Body covered throughout with numerous minute hairs and sparsely with long hairs. Carapace nearly as long as wide, with a slightly bilobed front. Two lateral spines on either side of carapace in hepatic region just posterior to orbit. No hooks on ischium of chelipeds.

DISCUSSION

The zoea of *E. limosum,* like other typical xanthid zoeae, is characterized by a long antenna with a reduced exopod. It is distinguishable from other known xanthid zoeae by stages 2 to 4 having a smooth antennal spinous process and two distinct outer spines on the telson. However, as the first stage zoea of *E. limosum* has a serrated antennal spinous process and three outer spines (2 lateral, 1 dorsal), it is difficult to distinguish from the first zoea of *Panopeus herbstii* Milne-Edwards, 1834. Only the strongly recurved extremity of the dorsal carapace spine in *Eurytium limosum* appears to distinguish the first zoeal stages of these two species.

Rathbun (1930) reported 18 species of crabs in the family Xanthidae from the coasts of Georgia and the Carolinas. Williams (1965), and Williams et al. (1968) added 8 more species, and Williams (1974) reported a new genus and species, *Allactaea lithostrota.* Thus, 27 species of xanthids belonging to 16 genera are now known to occur along the eastern coast of Georgia and the Carolinas. Larval stages of 12 species belonging to the genera *Leptodius, Panopeus, Neopanope, Hexapanopeus, Eurypanopeus, Micropanope, Rhithropanopeus, Menippe, Lobopilumnus, Pilumnus,* and *Eurytium* are now known from the eastern coast of North America. Larvae of the remaining genera (*Glyptoxanthus, Actaea, Domecia, Eriphia,* and *Allactaea*) known from this region remain undescribed. However, information on the larvae of *Eriphia* is available from other geographical areas (see Gurney 1942).

Wear (1970) concluded that the most important character of Lebour (1928) separating xanthid zoeae into recognizable groups was the length of the antennal exopod relative to the length of the protopodite. Scotto (1979) agreed with Wear (1970) in that a well-developed antennal exopod indicated a more primitive condition, and she mentioned the extra zoeal stage and the placement of male and female genital openings on the adults (after Guinot 1977) as evidence for the apparent "primitive" placement of the genus *Menippe.* If the antennal exopod is indeed a good character for placement within the family Xanthidae, *Eurytium limosum* is an advanced xanthid and is more closely allied to the genera *Hexapanopeus, Heteropanope, Neopanope, Lophopanopeus,* and *Rhithropanopeus.* Aikawa (1937) placed much phylogenetic significance on the antennal exopod and expanded the two xanthid zoeal groupings of Hyman (1925) into three groups. Rice (1980) has separated the known xanthid zoeae into four groups, employing the setation of the mouthparts as additional characters. The first of these groups, into which *Eurytium limosum* falls, contains the most advanced xanthids, with antennal exopods greatly reduced or absent.

The antenna of the first stage zoea of *E. limosum* is furnished distally with several spinules, but is smooth in later stages. This character, plus the presence of three outer spines on the telson of stage 1 zoea, indicates a not too distant relationship to less advanced xanthids such as *Panopeus herbstii.* The first stage zoea is similar to that of *Panopeus herbstii* Milne-Edwards, 1834 as described by Costlow and Bookhout (1961), but can be distinguished by the more strongly recurved distal portion of the dorsal carapace spine in *E. limosum.* The later stages resemble the zoea of *Rhithropanopeus harrisii* (Gould, 1841) as described by Connolly (1925), Chamberlain (1962), and Hood (1962), and the zoea of *Neopanope sayi* (Smith, 1869) as described by Hyman (1925, after Birge 1883) and Chamberlain (1957, 1961). However, the zoeae of *Eurytium limosum* have two outer spines on the telson in contrast to the single outer spine on the telson of *R. harrisii* and *N. sayi.*

Available data indicate that *Eurytium* may have originated from *Panopeus* stock but advanced along a separate line from those genera that have undergone a reduction in telsonal armature. There is, however, still some doubt as to the phylogenetic significance of many decapod larval characters. For example, according to the scheme of Aikawa (1937) and to the categorization of xanthid larvae by Rice (1980), *Panopeus bermudensis* Benedict and Rathbun, 1891 would rank as extremely primitive among the Xanthidae on the basis of its first stage zoea (Lebour 1944); it would likely deserve recognition under a separate genus were larval characters considered as phylogenetically significant as the adult morphology upon which its generic placement is presently based. This was noted by Wear (1970) and by Rice (1980).

Detailed descriptions of additional genera and species

likely will clarify questionable phylogenetic relationships among the many members of the Xanthidae. Future studies employing the larval characters given by Rice (1980) should, in particular, further clarify the phylogenetic significance of such larval characters as armature of the antennal exopod and telson within this group.

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January 1981

Growth Kinetics and Longevity of the Salt Marsh Rush *Juncus roemerianus*

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GROWTH KINETICS AND LONGEVITY OF THE SALT MARSH RUSH *JUNCUS ROEMERIANUS*

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ABSTRACT   Vegetative development of shoots of the tidal marsh rush *Juncus roemerianus* was studied quantitatively in short (S), medium (M), and tall-leaved (T) populations. Shoot longevity varied between populations, with some shoots producing one leaf and living 4 months, while others produced seven leaves and lived over 4 years. An equation was developed from plastochron and leaf-age determinations to estimate shoot age in each population studied. Major morphological events common to all populations were (1) cessation of growth of the first leaf produced on an erect stem when growth of the second leaf was initiated, and (2) death of the leaf from the tip downward. Although the time period was variable, growth rates of leaves equalled their death rates in each population during maximum periods of growth and subsequent decline. While growth and death rates were similar between two of the populations (M, T) investigated, these rates were vastly different from those representative of the third population (S). Growth and death kinetics for leaves on individual shoots involved cyclic phenomena represented by a series of greatly overlapping harmonic curves. Each shoot reached a maximum carrying capacity expressed as linear biomass. Although living portions were often distributed over three or four leaves, the total equated to two mature living leaves for the medium (M) and tall-leaved (T) populations. In the short-leaved population (S), the maximum amount of biomass attained by a single shoot during its life span equalled that of one mature leaf. A peculiar steady-state or homeostasis in growth and net productivity exists in each population. Short-lived shoots in the short-leaved population (S) was shown to have a rapid turnover of replacement rate, which is responsible for a high net productivity equal to or exceeding the net productivity of both the medium and tall-leaved populations. Although the cause of variation in basic growth patterns between the three populations was not investigated, both genetic and environmental factors may be involved.

INTRODUCTION

Tidal marshes are composed primarily of a herbaceous flora, the major constituents of which possess rhizomes. Through vigorous rhizome growth some of these herbaceous species dominate vast areas of tidal marsh. Black rush or needle rush, *Juncus roemerianus* Scheele, is a major constituent of tidal marshes located in estuaries on the South Atlantic and Gulf coasts of the United States (Eleuterius 1976a). Correspondingly, the species contributes to the energetics of many estuaries. Knowledge of shoot development, rates of leaf growth, and longevity of shoots is essential and basic to our understanding and assessment of net primary productivity, standing crop, and turnover of tidal marsh angiosperms. Estimates of growth, expressed as or based on standing crop, serve as a general index of comparison, but fail to reveal the details or kinetics of growth. Vegetative growth patterns of the major kinds of herbaceous plants are very different, although this fact has not been elaborated upon previously. Furthermore, there often appears to be considerable variation in growth rate, net primary productivity, and turnover between separated populations of the same species.

Steward (1968), Richards (1969), Dormer (1972), and Williams (1975) present excellent reviews of methodology and discussions on the quantitative analysis of plant growth, whereas Pratt (1941), Williams (1964), Williams and Rijven (1965), Koller and Kigel (1972), and Evans (1972) used successive linear measurements extensively to record and analyze plant growth.

The present work arose from previous studies to develop criteria for evaluating tidal marshes. We found that in some populations of *J. roemerianus* from 1 to 8 leaves were produced sequentially in a synchronized system from the erect stems and that these shoots bearing different numbers of leaves lived different lengths of time. In the present study, our objectives were to provide a reliable method of studying the developmental pattern of the shoot; to determine the morphological pattern of the shoot over a long period of time; to compare the growth rates of leaves, shoot longevity, and leaf death rates of representative plants in populations of *J. roemerianus* with very short, medium, and tall leaves (stand height); and to use the resulting data in estimating shoot age and turnover.

The three populations selected for study span the major structural characteristics of most populations of *J. roemerianus* in the coastal region bordering the northern Gulf of Mexico. These populations are located in tidal marshes at Belle Fontaine Beach (BFB), Grand Bayou (GB), and Salt Flats (SF) in the coastal area of Jackson County, Mississippi. Hereafter in this paper the above codes are used in reference to the location of the respective rush populations. The plants with shortest leaves but greatest density of shoots (N/m^2) are found in the SF population inhabiting areas with very sandy surface soil underlaid with clay at 2 to 4 feet. Rushes with leaves of medium length and density of shoots intermediate to those found at SF and BFB are found at GB. The soil at GB is a sandy clay. At BFB the

soils are highly organic, composed primarily of peat, and the plants have the longest leaves and lowest density of shoots. The soil water of the SF population is hypersaline (60 to 300 ppt). Soil water from the tidal marshes around GB is generally moderate-to-low in salinity (5 to 20 ppt) while that in the BFB marshes is relatively low (0 to 6 ppt) (Eleuterius 1974).

METHOD

Twenty young shoots, each bearing a first leaf less than 20 cm in length, were selected at random in each of the three plant populations. The shoots were marked with plastic rings and numbered during November 1976. Initiation of new leaves on each shoot was noted; the length of each live leaf and the length of the dead segment of older leaves were measured monthly for 28 months. A storm washed away our markers forcing us to conclude the study. Longevity of individual shoots and their respective growth curves (leaf length plotted against time) were determined from the obtained data and were compared to other shoots within and between populations.

RESULTS

Shoot Development

Sympodial branching characterizes the vegetative growth of mature plants of *J. roemerianus* (Eleuterius 1976b). As the rhizome apex turns upward, division of the apical meristem formed a rhizome apex (continuation bud) simultaneously with the production of an erect shoot. This growth phenomenon is also common to other angiosperms (Bennett-Clark and Ball 1951, Holttum 1955). Thus, the youngest shoot, bearing one leaf, is always proximal to the rhizome apex of an interconnected series of rhizomes and shoots, and the oldest shoot, often with three or more leaves, is the most distal to the apex (Figure 1A). The number of mature leaves produced on an individual shoot, along with other data to be given later, can be used to estimate the age of that shoot (Figure 1B) within a given population with relative precision. Young leaves of an individual shoot arise from short stems and grow through a slit in the base of the preceeding leaf in an alternating or distichous manner (Figure 1C).

Leaf Production and the Plastochron

The number of leaves produced on each erect stem was variable within and between the three populations (Table 1). About half of the shoots produced only one leaf in the SF and BFB populations. Erickson and Michelini (1957) described the plastochron as the time interval between two similar developmental events on the same shoot. Here the plastochron of *J. roemerianus* was variable and equal to the time required to produce one mature leaf.

Figure 1. Morphological characteristics of *Juncus roemerianus.* An interconnected series of rhizomes and shoots are shown in A. Younger shoots with fewer leaves are found near the rhizome apex, older ones farther away. B. Diagram of short erect stem connected to rhizome segment. Numbered, close-set nodes indicate origin of sequentially produced leaves on each erect shoot. C. The distichous or alternating arrangement of leaves on single shoot. Numbers correspond to sequence of leaf production.

TABLE 1.

Distribution of leaves on shoots of *Juncus roemerianus* in three different populations. Shoots are ranked according to total and average number of leaves produced on each shoot selected for study. Number of leaves indicates total or maximum number attained prior to shoot death or termination of the study.

Population	Number of Leaves per Shoot					
	1	2	3	4	5	X̄
Salt Flats (SF)	10	9	1			1.6
Grand Bayou (GM)	7	5	4	4*		2.3
Belle Fontaine Beach (BFB)	9	4	2	4*	1**	2.2

*One or more of these shoots may have produced a fifth leaf.
**This shoot may have produced a sixth leaf.

All second leaves were produced during the spring at SF, while in the GB and BFB populations, most second and third leaves were produced during the summer and following spring (1978), respectively (Figure 2). Although the seasonality

of secondary leaf production on individual shoots was similar for both GB and BFB, some shoots at BFB exhibited a precocious leaf development indicative of accelerated growth in very early spring.
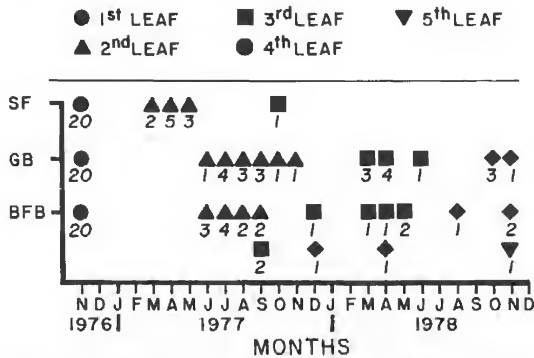

Figure 2. Populational differences in leaf production. Symbols indicate chronological order and array of leaf production on individual shoots. Subscripted numbers indicate number of shoots producing a second, third, fourth, or fifth leaf during a particular month.

Leaf Length

The range and average of the maximum heights (lengths) attained by mature leaves of *J. roemerianus* were distinctly different between the three populations as shown graphically in Figure 3. Leaves at BFB ranged from about 110 to 170 cm, and averaged 142 cm in length, and at GB from 65 to 133 cm, with an average of 104 cm. The population at SF had the shortest leaves, ranging from 11 to 64 cm and averaging 26 cm.

Leaf Growth and Death Curves

Representative growth and corresponding death curves for leaves produced on single shoots from three populations are shown in Figure 4. These size-versus-time plots show the cumulative increase in height (length) of successive leaves on three individual shoots, each of which represents a different population. The kinetics of shoot growth as shown in the BFB and GB curves are very similar (Figure 4: BFB, GB). Both illustrate several overlapping, yet, typical sigmoid curves with characteristic logarithmic (exponential), linear (grand), and senescent phases (Blackman 1919, Pope 1932). Plots of monthly averages from combined data (all shoots) for each population produced a similar but smoothed and flattened curve in comparison to that of individual shoots. Growth of the first leaf produced on an erect stem ceased when growth of the second leaf was initiated and represented a plastochron (Erickson and Michelini 1957). The process held for all subsequent leaves on an individual shoot and for all shoots producing more than one leaf in all populations.

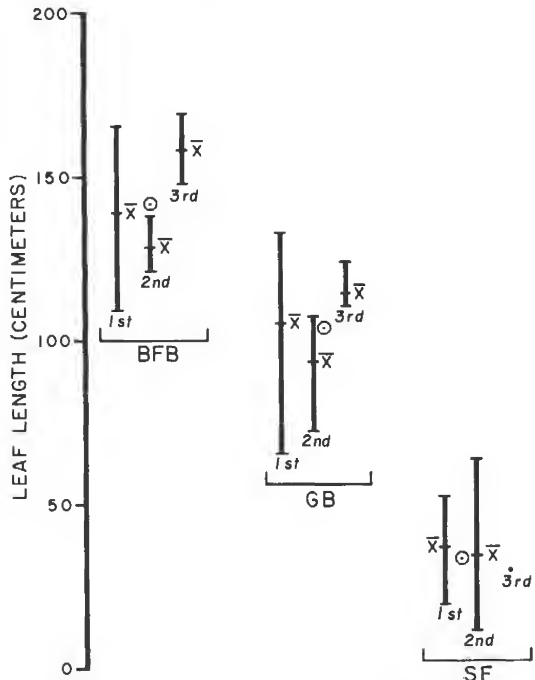As the second leaf matured the first leaf began to die

Figure 3. Populational differences in leaf lengths. Comparative data showing range and average mature leaf lengths for three populations studied. Circled dot ⊙ indicates average leaf length based on array of first, second, and third leaves produced in each population.

from the tip downward. This same relationship held between the third and second leaf and so on. Very little increase in leaf length occurred during winter months, whereas rapid growth characterized the late spring, summer, and early fall. Note the flattened curve for January and February in Figure 4. Although the reason for this is unclear, second leaves were generally slightly shorter than first or third leaves (see Figure 3). Growth of the third leaf began several months before the first and second were completely dead.

No consistent pattern was obtained for the curve representing senescence. The senescence phase of the growth curve often equalled the slope of the curve during the exponential phase, but senescence generally occurred very rapidly, represented by a graphically sharp decline. Death of leaf tissue represented by this steep decline in the senescent curve was not, however, restricted to any particular period of time and we could not assign any probable cause to it. Furthermore, there was a maximum amount of living leaf tissue sustainable on a single shoot and, although the living segments may have been distributed between two, three, or four leaves, the amount was not apparently greater than that of two entire living leaves representative of the mature component of the respective population. This observation held true regardless of the location of the population.

Dead leaves remain standing for several years or more in the BFB population, but are rapidly swept away by tides at SF. Fewer dead-standing leaves were found in the GB population in comparison with those at BFB.

Shoot development at SF is obviously an abbreviated process (Figure 4). Plots of all other SF shoots investigated are similar.
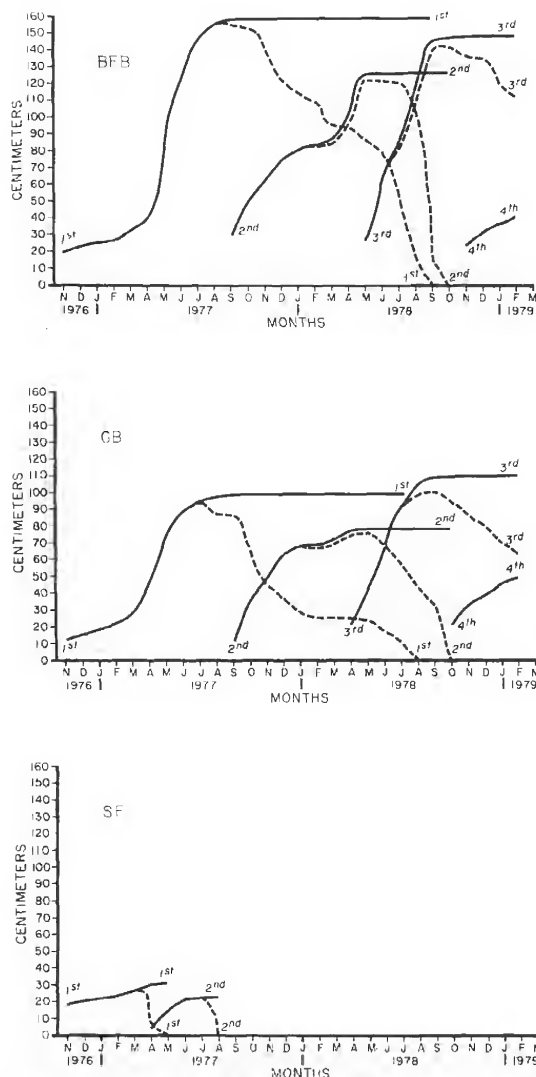

Figure 4. Growth and death curves for leaves produced on a single shoot of *Juncus roemerianus* in three different populations. Solid and dotted lines show size of the living portions of leaves versus time, the accumulative increase in leaf length, the sequential initiation of new leaves, the corresponding cessation of growth and senescence of leaves of representative shoots from each population.

Leaf Growth and Death Rates

Calculation of growth rates also indicated that the period of greatest leaf growth was during spring, summer, and early fall (Table 2). Average growth rates during this study period were very similar in the GB and BFB populations (about 0.7 and 1.0 cm per day, respectively). An average of 0.2 cm per day occurred during the period of maximum growth for the shoots observed in very early spring at SF. Although the growth rate of individual leaves was variable, we surmise that these estimates represent the exponential phase for new cohorts and, thus, are characteristic of the maximum sustainable or annual growth rate in the respective populations. The maximum daily growth of a single leaf in the BFB, GB, and SF populations and the months of occurrence were 1.5 cm (July), 1.1 cm (September), and 0.4 cm (February), respectively.

TABLE 2.

Average growth rate (cm/day) of mature leaves of *Juncus roemerianus* during the months in which maximum growth occurred (shown in parenthesis). Number of leaves used in determining growth rate of successive leaves on individual shoots shown in brackets.

Population	Leaf 1 (Mar, Apr, May)	Leaf 2 (Jul, Aug, Sep)	Leaf 3 (Apr, May, Jun)
Salt Flats (SF)	*0.2 [10]		
Grand Bayou (GB)	0.7 [13]	0.7 [8]	0.8 [4]
Belle Fontaine Beach (BFB)	1.0 [11]	1.0 [5]	1.3 [3]

*(Feb, Mar)

Calculation of death rates of leaves from the apex downward indicated that summer and fall were the periods of greatest leaf death (Table 3 and Figure 4) although some leaves died rapidly during winter. Average death rates during this period were also very similar in the GB and BFB populations (about 0.8 and 1.0 cm per day, respectively). An average of 0.7 cm per day occurred in late spring at SF. During this period death rate briefly exceeded growth rate. The maximum daily rate of death of a single leaf in the BFB, GB, and SF populations, and the months of occurrence were 4.2 cm (July), 2.2 cm (October), and 1.4 cm (May), respectively.

Leaf Longevity

Leaves of shoots in SF, GB, and BFB populations lived an average of 7.5, 16, and 14 months, respectively, based on all leaves on all shoots investigated. However, average age of leaves, based on shoots that produced more than one leaf, was 7, 14, and 12 months for SF, GB, and BFB, respectively

(Table 4). On shoots producing more than one leaf, the first leaf generally lived longer than the second in all populations examined. Third and fourth leaves usually lived as long as, or longer than, the second. Some leaves lived 22 months. Leaf longevity was very similar between the BFB and GB populations but contrasted sharply with that at SF.

TABLE 3.

Average death rate (cm/day) of mature leaves of *Juncus roemerianus* during the months in which maximum death occurred (shown in parenthesis). Number of leaves used in determining death rate of successive leaves on individuals shoots shown in brackets.

Population	Leaf 1 (Sep, Oct, Nov)	Leaf 2 (Jul, Aug, Sep)	Leaf 3 (Aug, Sep, Oct)
Salt Flats (SF)	*0.7 [9]		
Grand Bayou (GB)	0.6 [13]	1.0 [8]	†0.3 [4]
Belle Fontaine Beach (BFB)	0.9 [10]	1.4 [4]	†0.3 [3]

*(May, Jun)

†About one third of leaf was dead when experiment ended.

TABLE 4.

Leaf longevity. Average and maximum of months that leaves of *Juncus roemerianus* live in different populations. Leaves are grouped based on chronological development on individual shoots in each population. Number of leaves used in determinations shown in parenthesis.

Population	Leaf 1 X Max	Leaf 2 X Max	Leaf 3 X Max	Leaf 4 X Max	Leaf 5 X Max
Salt Flats (SF)	8 17 (15)	7 16 (8)			
Grand Bayou (GB)	15 22 (16)	13 17 (12)	15 16 (16)		
Belle Fontaine Beach (BFB)	15 22 (16)	11 14 (8)	11 15 (16)	12 14 (4)	15 (1)

Shoot Longevity

The number of leaves produced and the life span of each leaf on an individual shoot determine the longevity of that shoot. The shoots of the BFB and GB populations live about twice as long as those in the SF population (Figure 5). Mortality of shoots began 4 months after the study was initiated and continued periodically thereafter. The average shoot life at SF was 11 months with one shoot living 22 months. Average shoot life at GB was 25 months with seven shoots alive at the end of 28 months. Projected longevity, based on average life span and vitality of leaves studied in

the GB population, indicated that some of the shoots studied probably lived about 40 months. Although seven shoots were alive at the end of the study period, no new leaves were produced and those living leaves present were dying.
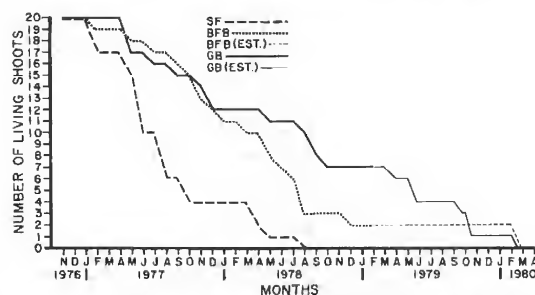

Figure 5. Shoot longevity. The life spans of three cohorts of shoots, each representative of a different population of *Juncus roemerianus*. Each cohort was composed of 20 shoots for a total of 60. Lines indicate mortality and survival of each group over time.

Similarly, the average longevity of shoots at BFB was 21 months with two shoots alive at the end of 28 months. Projected longevity, estimated from average life span and vitality of leaves from this propulation, indicated that 10% of the shoots may live about 40 months in the BFB population. Production of a sixth or seventh leaf certainly was possible on two of the shoots at BFB because both were very vigorous and new leaves had just been initiated. Moreover, shoots with six and seven leaves, which have been observed in the GB and BFB populations, respectively, clearly indicate that some vegetative shoots of the rush *J. roemerianus* may live 4 years or longer.

DISCUSSION

We found during this study that: (1) frequent linear measurements of leaf length are a valuable and sensitive aid in the interpretation of growth phenomena in *J. roemerianus*, (2) growth curves of an individual rush shoot are actually a complex network of overlapping curves or series of correlations between linear growth and time, (3) considerable variation in the kinetics of growth occurs between populations of *J. roemerianus*, (4) these populational differences appear to be caused by the location and the environmental conditions peculiar to respective populations, although it certainly was possible that they represented genetically distinct ecotypes, (5) our data provided basic information for making numerous types of estimates, such as: biomass, shoot age, leaf age, net productivity, and turnover in populations of *J. roemerianus*.

For emphasis, we found that developmental events of the shoot were repeated with the initiation of each new leaf and that the time intervals between leaves on the same shoot were highly variable. Therefore, the plastochron or time interval determined from the present study is equivalent to

the period required to complete the several developmental stages of one leaf (Erickson and Michelini 1957). Linear measurements of individual leaves and the plastochron age of shoots are nondestructive ways of obtaining data basic to net productivity estimates.

Although shoot development for the three populations examined is similar in the consistent morphological pattern of sequential leaf production and death, and in tracing the classical sigmoid growth curve, shoot characteristics are very different in other ways. These populational differences are summarized as follows: (1) leaf production—the number of leaves produced per shoot, (2) leaf length—the most obvious difference between the three populations, (3) leaf growth rate—equalled by leaf death rate within each population but variable between populations, and (4) leaf and shoot longevity—both lived much longer in the GB and BFB populations than at SF.

The BFB population is composed of plants with long leaves (110 to 170 cm, $\overline{X}$ = 142 cm) which remain standing for a long time after they die. About two thirds of the aerial standing crop are dead leaves. A smaller number of living shoots (about $500/m^2$) occupy the marsh surface at BFB in comparison to those found at GB ($700/m^2$) and SF ($2,000/m^2$) (Eleuterius 1980). The vitality of individual shoots at BFB is very different from one another with a small percentage of shoots in the population possessing great vigor and living several years. This contrasts with shoots in populations at GB and SF, where their growth patterns are most consistent. Furthermore, dead-standing leaves comprise about one fourth of the standing crop at GB in comparison to about one tenth of the vegetation at SF.

The vigor of individual shoots is, as with all tidal marsh plants, ultimately tied to the physical and chemical energetics of the estuary. Dead leaves readily accumulate in populations protected from high wind and wave activity; consequently, growth of living shoots is suppressed, probably because of competition for light. Populations exposed to frequent tidal action, where dead-standing leaves are readily swept away, are more apt to represent a steady state of continuous robust growth. The BFB population is in a protected location and consequently has a high ratio of dead to living leaves. The GB population is more exposed and the SF population is very exposed to wind, wave, and tidal action in comparison to that at BFB. Other environmental factors, such as the concentration of sea salts in the soil solution, obviously affect, to some extent, the growth of *J. roemerianus*.

In all of the populations studied, a reliable indication of the biomass can readily be obtained directly from plotted data. For example, there may be several living leaves on a shoot, but only one leaf increases its length at any living shoot, at any time. Therefore, the living component of leaves, which are not growing, decreases in size (linear measurement) because of leaf death. In the GB and BFB populations, the biomass sustained per shoot is equivalent

to that of two entirely living, mature leaves. However, this living tissue may be distributed over 3 or 4 leaves, depending on the stage of shoot development. The "two living leaves" concept represents the maximum carrying capacity of an individual shoot in these two populations. In each population studied, leaf growth essentially equals leaf death, separated in time by a certain linear quantity of living leaves, in the above instances: two leaves. The maximum carrying capacity or biomass for shoots in the SF population is equivalent to one mature leaf for the life of the shoot. The number of leaves sustained by shoots of *J. roemerianus* varies between different populations and has an inherent physiological basis (Watson 1952). An annual steady-state pattern of stability and equilibrium or homeostasis operates in each population of *J. roemerianus* and compares favorably with that reported by Williams and Murdoch (1972).

Since seasonal effects on leaf growth are minimal (Eleuterius 1974, 1976b), and because successive cohorts of new shoots are being produced in each population throughout the year, the average growth rate calculated for the cohort of shoots studied here during the periods of maximum growth is also the maximum sustainable growth rate. The period of active shoot growth is equivalent to maximum sustainable growth rate. The average rate of shoot growth is much less than the sustainable growth rate because the senescent leaf phase may be 2 to 4 times as long as the phase of active growth. The average rate of shoot growth calculated from total leaf length produced over shoot longevity showed a different rate than when calculated on the growth phase alone. For instance, at BFB the annual rate would be 0.5 cm/day, and at GB and SF the annual rates would be 0.3 cm and 0.1 cm/day, respectively. We feel that the maximum sustainable rates shown in Table 2 are accurate and more meaningful than annual rates shown above, especially in relationship to shoot growth and senescent patterns. Sustainable and average growth rates are obviously essential to an estimation of annual rates of growth.

Reliable estimates (E) of shoot age can be calculated from the number of leaves present on a shoot (N), the average plastochron (P), and average leaf longevity (L) for each population studied using the equation: $P (N - 1) + L = E$. For example: the age of a shoot that produced four mature leaves in the GB population would be approximately 38 months old, where $P = 8$, $N = 4$, $L = 14$. Similar estimates can be derived for shoots in the populations at BFB and SF. Comparison of estimates of shoot age with the actual age of a randomly selected group of tagged shoots from each population indicated that our method is reliable for any shoot within 1 or 2 months. Considering the wide variation in some populations of *J. roemerianus*, the method is very precise, has high usefulness, and represents a significant contribution to the biology of the rush.

The pattern of shoot production in *Spartina alterniflora* and *Scirpus olneyi* on the mainland coast of Mississippi

greatly contrasts with that of *J. roemerianus*. Generally all shoots within separate populations of the tidal marsh grass *Spartina alterniflora*, and sedge *Scirpus olneyi* arise simultaneously in the spring from the marsh surface in a synchronized manner in Mississippi. There are exceptions to this general pattern during years of mild winters. However, regardless of seasonality, all shoots within populations of *Spartina alterniflora* and *Scirpus olneyi* are about the same age. Consequently, all shoots reach maturity, produce flowers, and die at relatively consistent and predictable times within one year. This process, applicable to the Mississippi coast, may appear to contrast with reports on *Spartina alterniflora* by Hopkinson et al. (1978) for Louisiana, and Stout (1978) for Alabama. However, we feel that temperature differences related to latitudinal distances are responsible for these conflicting reports (Turner 1976). The lower part of Bayou La Fourche and Barataria Bay are located in the Mississippi River delta, a latitudinal distance of approximately 50 miles south of the Mississippi mainland coast. Stout (1978) worked in the marshes of Dauphin Island, a latitudinal distance of some 8 to 12 miles farther south than the mainland coast of Mississippi. However, Hopkinson et al. (1978) stated that *Spartina cynosuroides* and *Sagittaria lancifolia* have uniform developmental patterns represented by a single flush of growth. The point of our comparison here is to show that shoots of *J. roemerianus* are produced continuously, and mature and die in all seasons, whereas several other tidal marsh species have a single annual flush of growth. Thus, populations of the rush are composed of an array of shoots differing vastly in age. These wide ranges of shoot growth stages are described best and illustrated as a series of greatly overlapping harmonic curves. Changes in the vegetational structure of the rush stand cannot always be detected easily by direct observation or by sampling techniques like the Harvest Method. Each population of *J. roemerianus* is homogeneous as to vegetational structure, new shoots being initiated throughout the year while other, older shoots are dying. Therefore, only a small component or percentage of shoots composing the population die each year and these deaths span the entire year with a peak reached during late summer. Stout (1978) showed growth occurring throughout the year for *J. roemerianus* in Alabama.

Although seasonal conditions appear to affect individual shoots only moderately in our locale, these effects are generally not noticeable to the casual observer because all growth is suppressed equally on all shoots and the wide array of shoot growth stages obscures this process.

Furthermore, in some populations, e.g., SF, two entire crops of shoots may turn over every 22 months while in others a complete vegetational turnover may occur every 4 years. Alone, the total significance of this information would not be apparent. However, from preliminary studies on the same three populations of *J. roemerianus*, we learned that the recruitment of new crops of shoots or cohorts may

be six times greater in the SF population in comparison to that at BFB. Recruitment at SF appeared to be three times greater than at GB. This preliminary knowledge, combined with that of the present study, suggests an important pattern of growth. The SF population which seemingly would be a population of low productivity, based on standing crop estimates, may be one of very high net productivity, based on the large number of shoots per unit area of marsh and the rapidity of turnover. Although we are unable to develop fully these modes of production here because of incomplete recruitment and biomass data, it is important to mention that the net productivity of the very short leaved SF population may equal or exceed the net productivity in the very long leaved BFB population over the same period of time. We surmise that this phenomenon would not have been revealed by assessing standing crop from clip quadrats because the replacement shoots were obscured by dead shoots and the precision of the Harvest Method cannot measure these changes.

Our results agreed only in a general way with those of Stout (1978), Hopkinson et al. (1978), and Williams and Murdoch (1972), because our overall objective was different in that productivity as annual biomass or standing crop was not investigated. Stout (1978) used a combination of leaf counts and linear leaf measurements from random quadrats and related biomass for above ground to below ground determinations. Hopkinson et al. (1978) used standing crop from quadrats, and Williams and Murdoch (1972) used linear measurements of tagged leaves and standing crop making it more comparable to the present paper than the others. We disagree in the finer details of the growth kinetics reported by Williams and Murdoch (1972) in that there is no interval between the cessation of growth and onset of death, at least in the *J. roemerianus* of Mississippi. None of these papers showed clear patterns of shoot growth, longevity, senescence, and death. Furthermore, we feel that the compartments used in the production model of Williams and Murdoch (1972) were too broad: live leaves = all green, dying leaves (dead and green), and all dead. We have never seen mature leaves of *J. roemerianus* in Mississippi or elsewhere that were entirely green. Hopkinson, et al. (1978) stated that the *J. roemerianus* marsh they studied was in "transition" or changing vegetatively. They concluded their work by pointing out the difficulty of measuring "true net production" by the Harvest Method and the need for refinement in productivity techniques. Our paper presents techniques basic to improving future productivity work. Our method is much simpler, less time consuming, and more accurate than those previously used. Additionally, linear growth measurements, coupled with shoot demography and standing crop, may allow considerable clarification and insight into population structure, growth kinetics, and production of *J. roemerianus* tidal marshes.

In conclusion we emphasize that growth kinetics and longevity peculiar to *J. roemerianus* are vastly different between populations, and that high net productivity may be common to all populations of this tidal rush, although accomplished in different ways.

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Gulf Research Reports

January 1981

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EFFECT OF MINERAL DEFICIENCY ON THE GROWTH OF THE SALT MARSH RUSH *JUNCUS ROEMERIANUS*

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ABSTRACT   Plants of the salt marsh rush *Juncus roemerianus* were grown in deficient and complete nutrient solutions, and the growth responses were compared qualitatively and quantitatively. Plants grown in solutions deficient in K, S, P, and Mg were similar in appearance, which exemplified severe growth retardation. Plants grown in solutions deficient in Ca, N, and Fe also were very similar in total growth response, but had much longer leaves, more shoots, and greater biomass than those grown in the K, S, P, and Mg deficient solutions. Plants grown in complete nutrient solutions, with various sources of Fe, were very robust. Growth was better with $FeCl_3$ than with FeEDTA. The most robust growth occurred in plants grown in the nutrient medium deficient in micronutrients (B, Mn, Zn, Cu, Mo), indicating that *J. roemerianus* is very sensitive to specific or certain combined micronutrients or concentrations generally recommended for terrestrial, especially agricultural, plants. The qualitative and quantitative symptoms, such as color, length, and abundance of leaves and roots as a response to deficiency of specific elements, were similar to those deficiency symptoms previously described for numerous terrestrial plants. However, a deficiency of certain nutrients such as S and Mg has a much greater effect on *J. roemerianus* than is generally shown for terrestrial plants.

INTRODUCTION

Interest in mineral deficiency of agricultural plants has a long history and correspondingly voluminous literature (Chapman 1973a). Information is lacking on the effects of mineral deficiency on angiosperms inhabiting tidal marshes. This inadequacy probably exists because of the common assumption that most estuarine sediments contain an abundance of nutrients for plant growth. However, Adams (1963) found that plants of *Spartina alterniflora* become chlorotic in iron-deficient soils but marsh plant species found at higher elevations, such as *Distichlis spicata* and *Juncus roemerianus*, are unaffected. He also pointed out that *S. alterniflora* reponds to experimental foliar applications of ferrous sulphate or the addition of iron to a saline nutrient solution and is often restricted to low elevation marshes where the mean soluble iron content is in excess of 4 ppm. Adams (1963) also suggested that iron deficiency may limit the growth of *S. alterniflora* at high marsh elevations, because the greatest tendency toward chlorosis is in the higher, better-drained, rather than the lower, wetter sites.

Tyler (1967) obtained a significant growth response from *Juncus balticus* in salt marsh plots treated with ammonium on the Baltic coast, indicating that the rush species grew naturally in depauperate soils in which the nitrogen concentration was not optimum. Furthermore, the substrata of salt marshes are highly variable in structure, ranging from organic peat to sand, which consequently reflects considerable variation in nutrient composition (Grim 1968; Richards 1969; Buckman and Brady 1969; Chabreck 1972; Cotnoir 1974; Boyd 1970; Brupbacher et al. 1973; Eleuterius 1972, 1974). Additionally, certain plants

have relatively high or specific mineral requirements suggesting that soil nutrient deficiencies (low concentrations) may limit their growth (Brownell 1965, Rorison 1968, Wallace et al. 1966, Broyer et al. 1954). Zonation of flowering plants in coastal marshes has been shown to be influenced by mineral nutrition (Pigott 1969). Eleuterius (1974) observed red streaks on the leaves of numerous small plants of *Juncus roemerianus* which may have indicated a deficiency of phosphorous in some sandy, marsh soils. Sandy soils of salt flats, in contrast, did not appear to be deficient because dwarf plants with very dark-green leaves also were observed there.

The objectives of this study regarding the mineral nutrition of *Juncus roemerianus* were (1) to determine the individual qualitative and quantitative effects that seven deficient minerals and an array of micronutrients would have on growth of the rush, (2) to compare these responses to those obtained in complete nutrient solutions, (3) to assess and rank the resulting condition of the test plants, and (4) to evaluate the nutritional requirements of the tidal marsh plant.

MATERIALS AND METHODS

Standard nutrient media (Machlis and Torrey 1956) were used to determine the effects of mineral deficiency on *J. roemerianus*. Seven nutrient solutions were prepared, each deficient (−) in one of the following elements: nitrogen (N), phosphorus (P), potassium (K), sulfur (S), calcium (Ca), iron (Fe), and magnesium (Mg). One solution deficient in an array of micronutrients (B, Mn, Zn, Cu. Mo) also was prepared as a test medium. Two complete nutrient solutions, differing in the source of iron, also were prepared as controls. One complete nutrient solution contained $FeCl_3$, and another the chelated form FeEDTA. Distilled water also was used as a control. Plants grown from seed collected

from a single parental plant to reduce genetic variability were used in triplicate for each culture solution. The experiment was carried out during the spring in a greenhouse. Temperature varied from about 18°C to 30°C during the experiment.

Seedlings of similar size were selected, based on the number of leaves and leaf length, from a large number of seedlings grown as individual units. Roots were thoroughly washed and freed of all peat and other organic material, and then placed in clean (washed) river sand for 5 weeks. A dilute (1%) solution of 10-30-20 soluble fertilizer (Robert Peters Co. Inc.) was used in a single application as a nutrient source. Prior experience showed that this procedure resulted in a proliferation of new roots, which replaced those lost and injured in the initial washing.

New roots formed within a few weeks and the remaining old ones subsequently were easy to clean. Seedlings were carefully rinsed six times in distilled water. The number and length of leaves were determined. For statistical comparison, a "total" leaf length was obtained by adding the length of all leaves on each plant. A single plant then was placed in each battery jar filled with nutrient media and supported with specially prepared, waxed, plywood covers (Machlis and Torrey 1956). Observations were made weekly for survival and deficiency symptoms, and the general condition of the plants was recorded. Distilled water was added to the nutrient solutions as needed. At the end of 68 days, number of leaves, total leaf length, maximum leaf length (plant height), dry mass of leaves, maximum root length, and dry mass of roots were determined. Multidimensional plotting, a method of cluster analysis (Andrews 1972, Nance et al. 1975), was used for statistical analysis of the quantitative data representing the seedling at the beginning and at the end of the experiment. Statistical significance between treatments was tested by a 1-way analysis of variance (ANOVA) test and a least significant difference (LSD) test.

RESULTS AND DISCUSSION

Seedlings were shown to have no significant difference at the beginning of the experiment by a 1-way ANOVA statistical test. Multidimensional plots also showed similarity between the seedlings for number of leaves, maximum leaf length (plant height), and total leaf length (Figure 1). Qualitative characteristics of the plants in each treatment at the end of the experiment are shown in Table 1. The ANOVA test, which compared all test groups for each variable simultaneously, showed a statistically significant difference between the 11 groups, except for the number of leaves produced per plant (Table 2). This means, because of the nature of the ANOVA test, that at least one test group was statistically different from at least one of the other groups. However, the ANOVA test does not indicate which groups were significantly different. When the resulting data were subjected to a LSD test all measured variables were shown to have a significant difference between certain test groups.
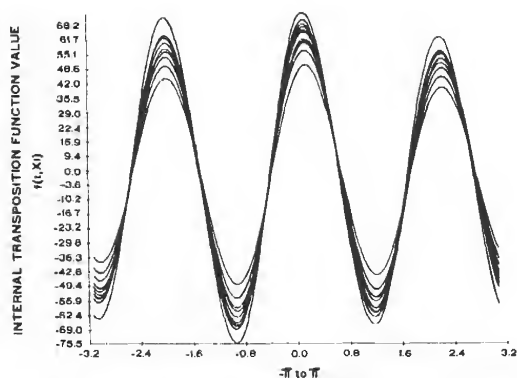

Figure 1. Multidimensional computer plots using the number and length of leaves for seedlings of *Juncus roemerianus* immediately prior to placing in complete and deficient nutrient solutions. Similarity and closeness of plotted lines indicate that plants are similar in size.

TABLE 1.

Mineral deficiency symptoms. Plant groups are ranked by treatments according to qualitative characteristics.*

— **Micronutrients**   Leaves dark green. Minimal dead leaf tissue. Roots white or light tan, about 25 cm long, with pliable root hairs. Root hairs slightly shorter (2—8 cm) than those in complete FeEDTA.

Complete (FeCL$_3$)   Leaves dark green. Very little (about 1%) dead leaf tissue. Roots white to light tan, 30 to 40 cm long, with obviously more mass than roots of plants in complete FeEDTA. Root hairs long (4—10 cm), pliable.

Complete (FeEDTA)   Leaves dark green. Very little (about 5%) dead leaf tissue. One plant dead. White to light tan roots, about 25 cm long, with long (4—10 cm), pliable root hairs.

— **Ca**   Leaves dark green, some dead young leaves. Roots short (10—15 cm), reddish-brown. Short stumpy root hairs about 0.5 cm long.

— **N**   Leaves pale or light green, about 15—20% dead leaf tissue. Roots white to light tan, very long (about 60 cm). Root hairs about 2 cm in length.

— **Fe**   Leaves brownish-yellow with four pale or light-green leaves, about 40% dead tissue and 50% dying, 10% living. Roots, white to tan, coarse, about 15 cm long. Short root hairs about 0.5 cm long.

— **K**   Leaves dark green, 25% dead leaf tissue (primarily young leaves). Roots long (30—35 cm), reddish-brown. Root hairs long (2—8 cm).

— **S**   Leaves dark to light green. About 15% leaf tissue dead. One plant almost dead (very little growth). Roots reddish-brown to tan, about 25 cm long. Root hairs coarse, less than 1 cm long.

— **P**   Leaves dark green, some leaves deep purplish-red or dark green with streaks of red. About 20% leaf tissue dead. One plant dead. Roots reddish-brown to tan. Few roots formed but extremely long, about 60 cm. Root hairs sparse, long (2—10 cm).

— **Mg**   Leaves yellow-green. Leaf tissue, 10% dead, 70—75% dying. Roots short (about 15 cm), light tan. Root hairs short, about 0.5 cm.

Distilled H$_2$O   Leaves light-green to yellow, brown or mottled with yellow or light to dark brown. About 20% leaf tissue dead, the remainder dying. Roots reddish-brown, short (10 cm), coarse. Root hairs short (0.5 cm) except on extreme tips of roots.

*Three plants were grown in nutrient media for 63 days.

TABLE 2.

Mineral nutrition characteristics of *Juncus roemerianus*. Plant groups are ranked by treatments according to quantitative characteristics. Values represent mean and standard error of the mean of three plants grown in nutrient media for 68 days.

Nutrient Solution	Number of Leaves	Total Leaf Length (cm)	Leaf Length Maximum (cm)	Dry Mass Leaves (g)	Root Length Maximum (cm)	Dry Mass Roots (g)
− Micronutrients	22 ± 3.2	732.4 ± 78.1	78.1 ± 2.8	2.790 ± 0.08	28.3 ± 3.7	0.421 ± 0.02
Complete FeCL$_3$	15 ± 2.5	415.2 ± 31.2	65.9 ± 5.9	1.593 ± 0.06	39.5 ± 5.0	0.313 ± 0.01
Complete FeEDTA*	12 ± 5.9	348.0 ± 198.7	49.0 ± 13.2	1.383 ± 0.72	27.7 ± 10.2	0.286 ± 0.10
− Ca	12 ± 3.1	255.2 ± 44.0	48.0 ± 5.7	1.103 ± 0.04	15.9 ± 0.3	0.164 ± 0.03
− N	13 ± 1.7	257.9 ± 10.7	44.9 ± 4.2	0.763 ± 0.01	70.2 ± 4.1	0.457 ± 0.08
− Fe	14 ± 1.2	212.6 ± 41.9	27.5 ± 4.7	0.413 ± 0.09	14.9 ± 4.3	0.081 ± 0.01
− K	8 ± 0.3	241.4 ± 12.5	56.1 ± 5.8	0.869 ± 0.11	37.1 ± 2.8	0.108 ± 0.01
− S†	9 ± 2.4	200.5 ± 62.6	36.8 ± 4.2	0.734 ± 0.29	25.0 ± 5.4	0.165 ± 0.11
− P*	9 ± 2.6	194.8 ± 69.1	38.0 ± 5.2	0.614 ± 0.27	56.1 ± 22.0	0.331 ± 0.17
− Mg	9 ± 1.2	186.7 ± 25.2	36.9 ± 1.9	0.435 ± 0.09	18.0 ± 2.0	0.075 ± 0.01
Distilled H$_2$O	11 ± 2.4	90.8 ± 16.0	19.9 ± 0.5	0.240 ± 0.04	11.3 ± 2.4	0.082 ± 0.02
F$_{(10,22)}$	1.97	5.34††	8.13††	7.84††	5.18††	3.44††
LSD$_{0.05}$	7.7	205.0	16.2	0.716	22.3	0.211

*Contained 1 dead plant.   †Contained 1 plant which was almost dead.   ††Significant at the 0.05 level.

We believe the LSD test indicates a better analysis than the ANOVA test for our purposes because it compares each group of values against every other group individually for each variable (Table 2). Furthermore, all variables, which included all groups, were subjected to cluster analysis or multidimensional plotting (MDPLT). This analysis compares and evaluates collectively and simultaneously the entire array of data. MDPLT evaluates all variables measured for each group, resulting in an averaged or total value for each test group. The group values are then ranked. Ranking all quantitative responses by MDPLT resulted in six distinctly different groups as shown in Figure 2. The closer the curves, the more closely related or similar were the test plant groups based on total response (all variables).

The most unexpected response was the robust growth of plants in nutrient medium without micronutrients (B, Mn, Zn, Cu, Mo). Table 2 shows that the longest leaves and greatest dry mass were produced on plants without micronutrients. Plants grown in both complete nutrient media were also robust, but the best growth was achieved with FeCl$_3$ rather than FeEDTA. Iron appeared to be necessary for strong root development in *J. roemerianus*. Plants in Fe, K, and Mg deficient media had very poorly developed root systems (Table 2).

Although chelation (FeEDTA) may ensure availability of Fe to terrestrial plants (Steiner and Van Winden 1970), the requirement of *Juncus roemerianus* is apparently more readily satisfied by the FeCl$_3$ source. Apparently most of the Fe of FeCl$_3$ became chemically bound in soils and in nutrient media, where it precipitated out of solution. Chemically bound Fe was not available for plant growth (Brown 1961, Hewitt 1963). Conversely, *J. roemerianus* may have a low Fe requirement and a high concentration of Fe in the nutrient medium or soil may have a toxic effect.

Plants grown in solutions deficient in Ca, N, and Fe had similar responses. These plants had shorter leaves, about one half of the number of shoots (reflected as a threefold
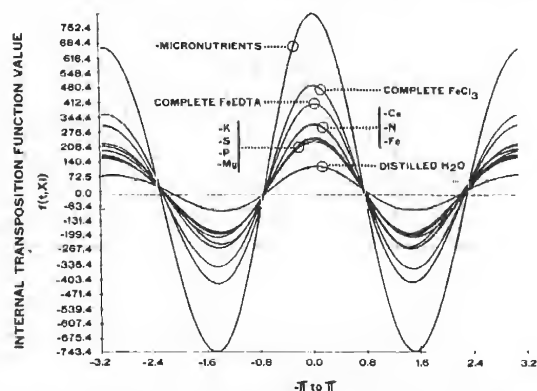

Figure 2. Multidimensional plots of plants of *Juncus roemerianus* grown in complete and deficient solution cultures for 68 days. The dotted, horizontal lines indicate the relative size of young plants at the beginning of the experiment. Curves shown in Figure 1 would center on the middle and fall within the upper and lower dotted lines. These dotted lines are provided to show the relative amounts of plant growth. Each curve represents the combined and relative condition of three plants in a particular series (triplicate) of deficient or complete nutrient media.

reduction in total leaf length), and one half of the biomass compared with plants in media without micronutrients. Plants grown in media deficient in K, S, P, and Mg were similar in appearance and all had a retarded growth habit.

Plants grown in distilled water were severely retarded compared to other plants. *J. roemerianus* appears to have a great capacity for survival under extremely depauperate conditions because the plants placed in distilled water survived and increased slightly in size, obviously utilizing stored nutrients. Gallagher (1975) stated that *J. roemerianus* was capable of storing reserves of nitrogen in leaves (luxury supply or reserve) without an observable increase in plant size. It was possible that the distilled water contained trace amounts of nutrients but certainly not at concentrations to support growth or survival.

The results of the present study indicate that the presence of Mg, P, S, and K, which are found in great quantities in highly organic tidal marsh soils (Pomeroy et al. 1969, Tyler 1971, Brupbacher et al. 1973), are extremely important for growth of *J. roemerianus*. The presence of Fe, N, and Ca are also very important for growth, but are probably required in much lower quantities than other nutrients. The growth of *J. roemerianus* was suppressed in solutions with micronutrients. Apparently, one or more of the micronutrients was inhibitory to *J. roemerianus*. Variable soil fertility accounts, at least in part, for length of leaves (stand height), rhizome and root development, inflorescence size, and other phenotypic characteristics which are known to vary between populations of *J. roemerianus* found in Gulf and Atlantic coastal marshes (Eleuterius 1975). The qualitative and quantitative diagnostic symptoms of the rush *J. roemerianus* are very similar for each treatment to those mineral deficiency symptoms generally described for many agricultural and terrestrial plants (Epstein 1972, Devlin 1966, Chapman 1973b), with the exception of an apparent sensitivity to certain heavy metals. These similarities in physiological responses to an array of deficient elements links the intertidal and estuarine *J. roemerianus* to the adjacent upland or terrestrial flora. However, the effects are different in *J. roemerianus* in comparison to those generally seen in terrestrial plants especially in regard to the degree of severity. For example, the absence of Ca apparently

had less of an effect on the growth of *J. roemerianus* than that described for terrestrial plants (Chapman 1973b, McMurtrey 1932). The growth of *J. roemerianus* was severely retarded by a deficiency of S and Mg, while such a severe effect on growth has not been generally described for terrestrial plants (Carolus 1935, Embleton 1973). The S and Mg requirements of *J. roemerianus* were much greater than those of most terrestrial plants.

The greater S and Mg requirements of *J. roemerianus* compared to those for terrestrial plants are obviously related to the higher concentrations of those elements in salt water and soils of tidal marshes. Furthermore, concentrations of P and K are much higher in the soils of tidal marshes than in those of most terrestrial areas. In contrast, there is little available Ca, N or Fe in estuarine waters or tidal marsh soils. The micronutrients B, Mn, Zn, Cu, and Mo occur in very low concentrations in the relatively pristine aquatic habitats of estuaries and tidal marshes in comparison to the concentration of the respective nutrient medium used in this study. The abundance of water probably accounts for the dilution of naturally occurring micronutrient concentrations in tidal marshes. The present study indicates that *J. roemerianus* is well adapted to the peculiar concentration and array of mineral nutrients in the soils and saline waters of pristine tidal marshes.

The heavy metals B, Mn, Zn, Cu, and Mo are compounds of domestic and industrial effluent which enter into estuaries from factories, municipalities, and through runoff from highways, marinas, farms, lawns, etc. Therefore, the sensitivity of the salt marsh rush *J. roemerianus* to heavy metal concentrations recommended for the culture of agricultural plants has profound and far-reaching importance to the future of estuaries, and indicates that *J. roemerianus* is physiologically distinct. The latter is not surprising because of the long evolutionary history of halophytes, and it points out the need for further physiological studies on *J. roemerianus* and other tidal marsh plants.

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Ichthyofaunal Colonization of a New Artificial Reef in the Northern Gulf of Mexico

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ICHTHYOFAUNAL COLONIZATION OF A NEW ARTIFICIAL REEF IN THE NORTHERN GULF OF MEXICO

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ABSTRACT Ichthyofaunal colonization of a new artificial reef was monitored from June 1975 through September 1977. Direct observations were accomplished using SCUBA. Theories of colonization and species equilibrium of islands and islandlike habitats were applied to the colonization data from the artificial reef. Sixty species of fishes from 33 families were recorded at the reef. Fifty-two percent of these species were primary reef fishes and 48% were secondary. Colonization data were produced only from the occurrence of primary reef fish. Data indicate that ichthyofaunal communities in the northern Gulf of Mexico are heavily influenced by seasonal changes in temperature, and that colonization by reef fish in that area does not conform to theories of immigration and extinction for island biotas. These results concur with similar work conducted on reef ichthyofauna in the eastern Gulf of Mexico.

INTRODUCTION

Ichthyofaunal colonization of a new artificial reef in the northern Gulf of Mexico was conducted from June 1975 through September 1977.

Theories of colonization and species equilibrium of islands and islandlike habitats have been discussed by MacArthur and Wilson (1967), Simberloff (1968), and Shoener (1974a, 1974b). Cairns et al. (1969) developed a method of estimating rates of immigration and extinction, calling them colonization and decolonization rates, respectively. Smith (1979) applied these theories to the ichthyofaunal colonization of patch reefs in the eastern Gulf of Mexico.

This study attempts to apply the above theories of colonization and species equilibrium of island habitats to the colonization of a Liberty ship artificial reef in the northern Gulf of Mexico.

METHODS AND MATERIALS

This study was conducted on the scrapped hull of the BENJAMIN WATERHOUSE, a World War II Liberty ship. The scrapped ship, sunk on June 10, 1975, lies in 14 m of water about 8 km south of the western end of Horn Island (Figure 1), and represents approximately 76,200 m^2 of hard substrate.

Monthly ichthofaunal observations began on July 21, 1975, using conventional sportfishing techniques and SCUBA diving. Hydrographic data, including temperature and salinity, were obtained for surface and bottom water masses during each survey. Turbidity of surface and bottom water masses was measured using a secchi disc.

A list of fish species for each observation dive was compiled on underwater paper attached to a clipboard. Also, a debriefing session for divers/observers was held immediately after each dive.
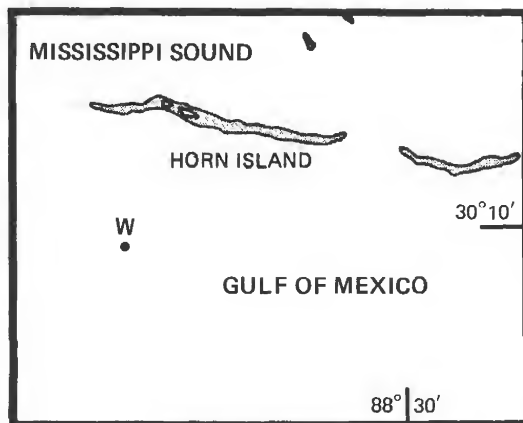
Figure 1. Waterhouse Reef (W) site.

A list was compiled of all species of fishes observed on any part of the artificial reef, and it included estimates of size and abundance. Whenever identification of a fish was uncertain, attempts were made to capture the specimen using hand nets, pole spears, and slurp guns.

Turbidity was highly variable. Whenever water clarity was adequate, 35 mm photographs were taken of reef fishes. When water visibility was less than approximately 3 m, no sampling was conducted due to increased difficulty in making accurate observations.

RESULTS

Hydrography

Temperature and salinity from surface and bottom water were measured monthly at Waterhouse Reef from July 1975 through September 1977 (Table 1). Bottom water visibility ranged from 0 to 14 m. These data compare favorably with data from previous years (Christmas and Eleuterius 1973).

TABLE 1.

Surface (S) and bottom (B) water temperatures (°C), and salinity (ppm) at Waterhouse Reef.

| Month | 1975 | | | | 1976 | | | | 1977 | | | | 1978 | | | |
| | Temperature | | Salinity | | Temperature | | Salinity | | Temperature | | Salinity | | Temperature | | Salinity | |
	S	B	S	B	S	B	S	B	S	B	S	B	S	B	S	B
January	–	--	–	–	–	--	–	–	–	–	–	--	–	–	–	–
February	–	--	–	–	14.3	17.0	32.0	35.0	–	–	--	–	–	–	–	–
March	–	--	–	–	19.0	19.0	26.0	34.0	–	–	–	–	–	–	–	–
April	–	–	–	–	23.1	20.4	19.0	34.0	21.0*	19.0	23.0	35.0	–	–	–	–
									24.0	22.5	28.0	31.0				
May	–		--	–	24.2	22.0	27.0	35.0	25.0	24.0	18.0	28.0	–	-	–	–
June	–	–	–	–	25.3	23.1	24.0	30.0	28.0	25.0	28.0	34.0	–	–	--	--
July	28.8	25.8	29.5	35.0	28.6	22.0	26.0	38.0	30.0	30.0	34.0	35.0	–	--	--	–
August	20.0*	26.9	24.0	32.0	–	–	–	–	–	–	..	–	–	–	–	–
	30.0	25.8	24.0	38.0												
September	29.5	29.5	28.0	28.0	29.2*	28.6	32.0	34.0	30.0	29.0	31.0	32.0	–	–	–	–
					27.0	27.5	30.0	31.0								
October	22.8*	23.0	28.0	29.0	24.7	25.3	33.0	33.0	–	--			–	–	–	–
	23.0	23.0	25.0	30.0												
November	23.0*	23.0	28.0	30.0	19.2	19.8	32.0	30.0	–	–	–	--	22.0	25.0	32.0	32.0
	19.3	19.8	33.0	34.0												
December	16.0	17.8	29.0	31.0	14.0*	15.0	29.0	29.0	–		–	–	–	–	--	–
					13.0	15.0	30.0	38.0								

*Hydrography measured twice in month.

Species Composition

All fishes identified from Waterhouse Reef were classified according to Starck (1968) into two groups: primary reef fishes, and secondary reef fishes (Table 2). Primary reef fishes are those which almost exclusively are found inhabiting reef or reeflike habitats. Secondary reef fishes are those which can be found on reefs but are more numerous at other habitat types, i.e., grassbeds, sand or mud flats, or open water. Smith (1976), working in the eastern Gulf of Mexico, also used the groupings developed by Starck (1968). For those species not covered by Starck or Smith, I consulted work by Hastings (1972), Christmas et al. (1973) Walls (1975), and Hoese and Moore (1977).

Sixty species of fishes from 33 families occurred at Waterhouse Reef (Table 2). Fifty-two percent were primary reef fishes and 48% were secondary reef fishes. Nearly half of the secondary reef fish group was composed of pelagic species.

Colonization of Primary Reef Fish

Colonization of a habitat and the approach of species equilibrium within that habitat can be followed by calculating immigration and extinction rates, described by the rate at which new species enter a habitat and old species leave it. Lapses of time between observations in this study made it impossible to calculate the actual rates of immigration and extinction. Therefore, I followed a method developed by Cairns et al. (1969) for calculating colonization and decolonization rates, a method which compensates for those time gaps between observations.

The colonization curve, colonization rate curves, and decolonization rate curves (Figures 2, 3, 4, 5, and 6) were produced from the occurrence of primary reef fish listed in Table 2.

The colonization curve (Figure 2) increased rapidly during the first 14 months of the study, then began to level off, and finally achieved an asymptote at the 17th month. The colonization rate for Waterhouse Reef was calculated by combining new species per observation with recurring species (those species which disappeared from the reef but later reappeared), and dividing by the amount of time between observations. Figure 3 represents the rate of colonization of fish species per day (scatter plot) plotted over the duration of the study. An exponential curve (solid

Figure 2. Colonization curve for Waterhouse Reef.

TABLE 2.

List of fish species from Waterhouse Reef classified as primary and secondary reef fishes following Starck (1968).

PRIMARY REEF FISH

Antennariidae
Antennarius ocellatus. . . . .
Ocellated frogfish

Serranidae
Centropristis philadelphica. . . . .
Rock sea bass
Diplectrum formosum . . . . Sand perch
Epinephelus nigritus . . . .
Warsaw grouper
Mycteroperca microlepis . . . . Gag
Serraniculus pumilio . . . .
Pygmy sea bass
Serranus subligarius . . . .Belted sandfish

Grammistidae
Rypticus maculatus. . . . .
Whitespotted soapfish

Priacanthidae
Priacanthus arenatus . . . . .Bigeye

Apogonidae
Apogon pseudomaculatus . . . .
Twospot cardinalfish

Lutjanidae
Lutjanus campechanus . . . Red snapper
L. griseus. . . . . .Gray snapper
L. synagris . . . . Lane snapper

Pomadasyidae
Haemulon aurolineatum . . . . .Tomtate
Orthopristis chrysoptera . . . . . .Pigfish

Sparidae
Archosargus probatocephalus . . . .
Sheepshead
Diplodus holbrooki. . . .Spottail pinfish
Lagodon rhomboides . . . . .Pinfish

Sciaenidae
Equetus umbrosus . . . . .Cubbyu

Ephippidae
Chaetodipterus faber . . . .
Atlantic spadefish

Chaetodontidae
Chaetodon ocellatus . . . .
Spotfin butterflyfish
Holocanthus bermudensis . . . .
Blue angelfish

Pomacentridae
Pomacentrus partitus . . . .
Bicolor damselfish
P. variabilis. . . . . . . Cocoa damselfish

Labridae
Halichoeres bivittatus. . . .Slippery dick
H. caudalis . . . . Painted wrasse

Sphyraenidae
Sphyraena barracuda . . . .
Great barracuda

Blenniidae
Blennius marmoreus . . . .
Seaweed blenny
Hypleurochilus geminatus . . . .
Crested blenny

Gobiidae
Gobiosoma longipala . . . Twoscale goby

Balistidae
Balistes capriscus . . . . Gray triggerfish

SECONDARY REEF FISH

Carcharhinidae
Carcharhinus maculipinnis . . . .
Spinner shark
Rhizoprionodon terranovae . . . .
Atlantic sharpnose shark

Sphyrnidae
Sphyrna sp. . . . . . Hammerhead shark

Clupeidae
Harengula jaguana. . . . . Scaled sardine

Ariidae
Arius felis . . . . Sea catfish

Antennariidae
Antennarius radiosus . . . .
Singlespot frogfish

Ophidiidae
Brotula barbata . . . . . Bearded brotula

Syngnathidae
Hippocampus zosterae . . . .
Dwarf seahorse

Serranidae
Diplectrum bivittatum . . . .
Dwarf sand perch

Pomatomidae
Pomatomus saltatrix . . . . . . .Bluefish

Rachycentridae
Rachycentron canadum . . . . . . Cobia

Echeneidae
Echeneis naucrates . . . . . Sharksucker

Carangidae
Caranx crysos . . . . .Blue runner
C. hippos. . . . . Crevalle jack
Seriola zonata . . . . . Banded rudderfish
Trachurus lathami. . . . . . .Rough scad
Vomer setapinnis . . . Atlantic moonfish

Coryphaenidae
Coryphaena hippurus. . . . . . .Dolphin

Sparidae
Stenotomus caprinus . . Longspine porgy

Sciaenidae
Bairdiella chrysoura. . . . . .Silver perch
Leiostomus xanthurus . . . . .Spot
Micropogonias undulatus. . . . .
Atlantic croaker

Scombridae
Scomberomorus sp.. . . . . . . Mackerel

Stromateidae
Peprilus burti . . . . . . .Gulf butterfish

Scorpaenidae
Scorpaena brasiliensis. . . . . .Barbfish

Bothidae
Paralichthys lethostigma . . . .
Southern flounder

Balistidae
Monacanthus hispidus . . . .
Planehead filefish

Tetraodontidae
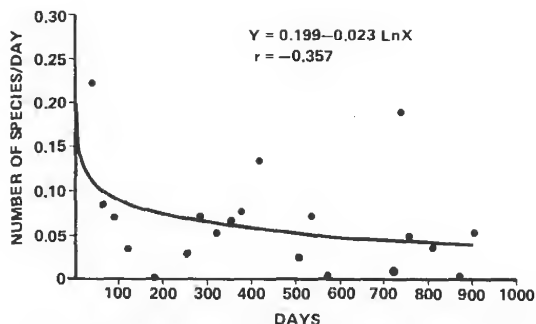*Sphoeroides parvus* . . . . . Least puffer

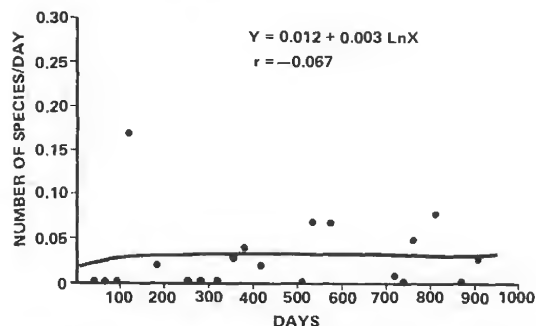Figure 3. Colonization rate for Waterhouse Reef (using recurring species).

Figure 4. Decolonization rate for Waterhouse Reef (with recurring species).
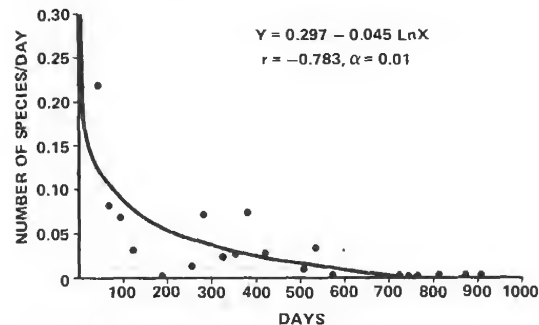

Figure 5. Modified colonization rate for Waterhouse Reef (without recurring species).

line) was fitted to the colonization rate by regressing the number of species colonized per day on the logarithm of time ($r = -0.357$). The decolonization rate (Figure 4, scatter plot) was calculated by determining the number of species eliminated from the reef per observation, and dividing by the time between observations. An exponential curve (solid line) was fitted to the decolonization rate by regressing the number of species eliminated from the reef per day on the logarithm of time ($r = -0.067$). Neither of these regressions proved significant ($\alpha = 0.05$).

Colonization and decolonization rates also were calculated for these data without considering recurring species. Instead, if a species disappeared and reappeared regularly, initial colonization was the only one considered. An exponential curve was fitted to the modified colonization rate (Figure 5) by regressing the number of new species per day on the logarithm of time ($r = 0.783$, $\alpha = 0.01$). An exponential curve was fitted to the modified decolonization rate (Figure 6) by regressing the number of species eliminated per day on the logarithm of time ($r = -0.390$, $\alpha = 0.10$)
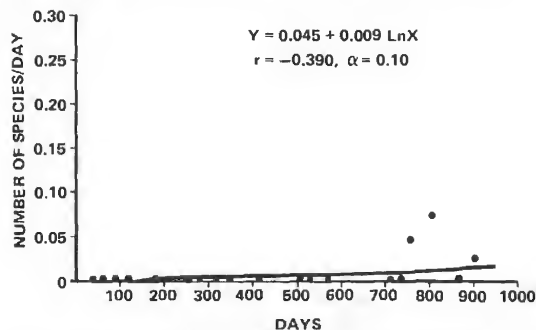
Figure 6. Modified decolonization rate for Waterhouse Reef (without recurring species).

DISCUSSION

Recruitment

Rate of recruitment of species (all species observed) to Waterhouse Reef throughout the 28 months of the study was approximately two species per month. A 28-month study of a Liberty ship reef in Alabama waters revealed a recruitment rate of almost five species per month (Crozier 1977), and an inshore jetty in northern Florida showed a recruitment rate exceeding eight species per month over 31 months (Hastings 1972). The Alabama and Florida artificial reefs mentioned apparently exhibited higher rates of recruitment because of their proximity to other recruitment areas and to deeper water. In each case, observed recruitment was decreased or eliminated during winter months, as reported in this study, but as water temperature increased above $20°C$, recruitment increased considerably.

Colonization and Species Equilibrium

MacArthur and Wilson (1967) postulated that an island community proceeds through a series of successional changes leading to a point of equilibrium whereby immigration of new species is offset by extinction of other species. At the point of equilibrium, species composition is dynamic over time, theoretically a slow process, as some species are replaced by others.

I classified Waterhouse Reef as an island because there is a vast expanse of flat bottom consisting of mud and silt surrounding the artificial substrate. The study reef is at least 9 km from the nearest hard substrate.

For this discussion, only primary reef fish species (Table 2) were considered. A species was considered an unsuccessful colonizer if it appeared only once.

Since observations of Waterhouse Reef ichthyofauna began immediately after the hull was sunk, the fish population was monitored from its inception through 28 months of colonization. Colonization of Waterhouse Reef was initially rapid and decreased with time. The cessation of colonization is illustrated by the asymptote on the colonization curve (Figure 2). The two depressions in this curve that precede the asymptote were the result of decreased recruitment of new species during winter months. Several species unsuccessfully attempted to colonize after month 17 of the study which could indicate that the maximum number of species for that habitat had been approached by that time. Some of these species, such as *Pomacentrus partitus* and *Halichoeres caudalis,* possibly reacted negatively to several factors in combination which resulted in their failure to colonize. Increased species number and temperature changes are possibly two of those factors, and a third factor may have been competition from congeners (*P. variabilis* and *H. bivittatus*) present prior to their arrival.

Smith et al. (1975) concluded that fluctuating water temperature, turbidity, red tides, and anoxia following phytoplankton blooms were the major stress factors operating on the ichthyofaunal communities in the eastern Gulf of Mexico. Temperature fluctuations appeared to be the major stress factor operating on the ichthyofauna of Waterhouse Reef. Decreasing water temperature during winter periods markedly affected the species composition of the study reef. Many species, such as *Pomacentrus variabilis, Chaetodon ocellatus,* and *Holocanthus bermudensis,* disappeared from the reef during the winter months. An influx of recurring species occurred as water temperature rose in spring and summer. Although the recruitment process of the recurring species was repeated each year, the resources sustaining a particular species were not being depleted by new species having the same niche requirements; therefore, competitive exclusion from the community was not occurring. Seasonal disappearance and reappearance of many of the same species at Waterhouse Reef could affect the pattern of colonization if recurring and new species were given the same importance. The colonization rate curve (Figure 3) does not accurately describe colonization of new species on the reef. The reason for this is the importance placed on recurring species in the formula used to calculate that rate.

The decolonization rate curve (Figure 4) also provides an inaccurate view of actual decolonization due to the recurring species phenomenon.

If seasonal reoccurrance of a species is not new colonization but rather is continued utilization of a resource already colonized, then it is necessary to consider the rates of colonization and decolonization disregarding recurring species. These modified colonization and decolonization rates are calculated as described above with the exception that recurring species are not given the same importance as new species. The modified colonization rate (Figure 5) adequately represents the colonization of new species to the study reef, and is consistent with the colonization theory as set forth by MacArthur and Wilson (1967). These findings agree also with those of Smith (1979), who did a similar study on patch reefs in the eastern Gulf of Mexico.

The modified decolonization rate (Figure 6) does increase with time as stated by the MacArthur-Wilson theory; however, there are factors which indicate that this curve does not represent the actual decolonization of Waterhouse Reef ichthyofauna. Six species reported as eliminated from the reef fauna were *Lutjanus synargris, Diplodus holbrooki, Epinephelus nigritus, Serraniculus pumilio, Holocanthus bermudensis,* and *Blennius marmoreus. Lutjanus synagris, D. holbrooki, S. pumilio, H. bermudensis,* and *B. marmoreus* frequently were present on the reef but were never abundant. I believe they probably were overlooked in sampling rather than actually eliminated from the reef fauna. *Epinephelus nigritus* was one of the initial colonizers and, with few exceptions, always was present during my observations. Juveniles of this species (200 to 250 mm total length) were recorded initially; however, the size of the fish observed increased with time during the study. As the size of fish observed increased, their abundance decreased. *Mycteroperca microlepis,* another grouper, began to colonize the reef in July 1976. It is possible that, due to the low numbers of *E. nigritus, M. microlepis* was able to displace the former. Because of behavioral differences between the two species, that conclusion is unlikely. Rather, it is more probable that *E. nigritus* was overlooked in sampling because of its decreased numbers and its secretive behavior. If these assumptions are valid, virtually no decolonization took place on the artificial reef during this study.

The dynamic species composition expected from the MacArthur-Wilson theory was not evident at Waterhouse Reef, but rather, as Smith (1979) found, species composition exhibited considerable stability, with 92% of the reef fish reported herein already having been colonized by the end of the first year. Those species continued to dominate the primary reef fish group throughout the remainder of the study.

CONCLUSIONS

My findings coincide with those of Smith (1979), indicating that reef-fish communities in the northeastern Gulf of Mexico do not conform to the MacArthur-Wilson model of immigration and extinction for island biotas. It was necessary to disregard recurrent species for these data to correspond to the findings of Smith (1979); however, I believe this was justified because of the strong seasonal

influence operating on the ichthyofauna of Waterhouse Reef, coupled with the lack of species replacement when life-sustaining resources were abandoned by a seasonally absent species. These findings in no way refute the theory proposed by MacArthur and Wilson (1967), and it is probable that the strong influence exerted by temperature changes on the study reef make such an equilibrium situation impossible to attain.

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Gulf Research Reports

Volume 7 | Issue 1

January 1981

Silica and Ash in Several Marsh Plants

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SILICA AND ASH IN SEVERAL MARSH PLANTS

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ABSTRACT   Ash and silica content and their depositional patterns in tissues of *Spartina alterniflora* Loisel., *Distichlis spicata* (L.) Greene, *Scirpus validus* Vahl., *Zizania aquatica* L., and *Limonium carolinianum* (Walt.) Britt. were determined. *Zizania aquatica* leaves had the highest silica content (6.0%) of any of the plant parts tested; silica making up over half of the ash. Silica in the plants was opaline in character. *Limonium carolinianum* did not accumulate silica in any great amount. However, ash content was very high in *Limonium carolinianum* and *Scirpus validus* making up over 17% of the dry weight of the leaves. X-ray diffraction showed the presence of halite (NaCl) and calcium sodium phosphate (2.4 CaO · 0.6 Na_2O · P_2O_5) in the ash of the leaves of all the plants from Mississippi except *Zizania aquatica*. Mineral deposition (silica and other minerals) in *Zizania aquatica* occurs in rows lengthwise of the leaf, and there are bowtie- and oval-shaped phytoliths. In *Distichlis spicata* leaves, mineral deposits occur in rows of elongate, serrated units. Spongy mineral deposition occurs lengthwise of the leaves of *Spartina alterniflora* and some of these deposits, including the silica, are fibrous. In *Scirpus validus* heavy deposits occur lengthwise of the leaf. Silica occurs in a sheetlike pattern and in rows of oval particles.

INTRODUCTION

Silica content of agricultural plants has been shown to be variable and to depend primarily on soil type and plant species (Jones and Handreck 1967, Lewin and Reimann 1969, Lanning and Linko 1961). Certain cultivated grasses such as rice may contain up to 20 times that of crimson clover *Trifolium incarnatum* (Russell 1961). Based on available information, monocotyledons generally have much more silica than dicotyledons (Metcalfe and Chalk 1950a, 1950b; Metcalfe 1960). Sangster (1978) suggested that the ability of plant species to absorb, transport, and deposit silica in similar aggregate formations may indicate a common origin or epicenter and subsequent migration of the species to other biogeographical realms. However, it is equally possible that the ability of a plant species to absorb and deposit silica within their tissues may have changed with evolution and migration to different regions.

Silica deposits in the aerial portion of crop plants contribute several beneficial effects. Leaves of rice are stiff and erect when silica content is high, but droop when it is low (Ishizuka 1971). Erect leaves are more photosynethetically active than drooping leaves (Ishizuka 1971); furthermore, high silica content enhances seed retention and prevents shattering, a common characteristic of grasses which complicates harvesting of seed in some species (McWilliams 1963). Lodging (bending of the culm: weak culm) of cereal plants also can be prevented by additions of silica to the soil (Mulder 1954). There is evidence that increasing the silica content of the soil (Monteith 1966) may cause a decrease in transpiration. A reduction in susceptability to fungal and insect attacks of rice and other gramineous crops has been attributed to a high silica content of the respective plants (Vlamis et al. 1958, Jones and Handreck 1967,

Ishizuka 1971). Relatively high concentrations of silica in plants also are known to prevent manganese toxicity, apparently by decreasing manganese uptake (Vlamis and Williams 1967). Rice plants with a high silica content also have a low iron content (Jones and Handreck 1967). High concentration of nitrogen or phosphorous in cultivated fields causes a decrease in the concentration of silica in barley, wheat, and other crops grown in those areas (Jones and Handreck 1967). Ponnamperuma (1964) has shown that silica improves oxygen supply to the root by increasing the volume and rigidity of gas channels in the root and shoot. Other edaphic factors such as soil pH also are known to affect silica uptake by cultivated plants. If those facts hold true for wild plant species, they have important implications regarding our understanding of natural ecosystems.

Little is known about silica content or the factors affecting silica uptake in wild plant species (Chen and Lewin 1969). The same distribution patterns and factors affecting silica deposition may or may not be similar between wild and cultivated plant species. There may or may not be major differences between silica content of terrestrial and aquatic species. Does the same plant species found in different geographical areas have the same silica uptake ability? Do native grasses and other wild monocotyledons, as present evidence indicates, have more silica as a rule than native dicotyledons? Furthermore, most work on native plants has been done on terrestrial species. To our knowledge no work has been done on floating or submerged aquatic plant species. Recently, however, Lanning and Eleuterius (1978) investigated silica content and depositional patterns of *Juncus roemerianus* Scheele, a common rush (Eleuterius 1975, 1976) of salt marshes of the South Atlantic and Gulf coasts. *Juncus roemerianus* was found to contain considerable opaline silica but no α-quartz. The amount of silica in plants corresponded to the amount found in soil, and silica content increased during the growing season. Lanning (1972)

showed that *Juncus interior* Weig and *Juncus bufonius* L., rush species of inland low areas, contained considerable silica, both opaline and α-quartz, and that silica content of *Juncus interior* increased nearly eightfold over the growing season.

The present study entailed five objectives: (1) to compare silica content of grass and sedge species from wetlands of different geographical locations; (2) to investigate silica content of grass and sedge species which grow under continuously but partially submerged conditions; (3) to compare silica content of several wetland monocotyledons with at least one dicotyledon from coastal wetlands; (4) to describe the silica depositional patterns in each species; and (5) to access the analytical results for these wetland plant species in view of knowledge of silica in agricultural plants. Specifically we were to determine: (1) the types and quantity of silica, if present, in several species of marsh plants, and (2) the ash (A) and silica (Si) contents of the various parts of the plants.

The four monocotyledons studied were *Spartina alterniflora* Loisel., *Distichlis spicata* (L.) Greene, *Scirpus validus* Vahl., and *Zizania aquatica* L. *Limonium carolinianum* (Walt.) Britt. was the dicot species analyzed. *Scirpus validus* and *Zizania aquatica* (wild rice) typically grow along rivers and bayous with the lower portion of the plants submerged. *Distichlis spicata, Spartina alterniflora,* and *Limonium carolinianum* are intertidal, with *Spartina alterniflora* occupying the lowest position on the tidal plane.

METHODS AND MATERIALS

Zizania aquatica was collected from Pascagoula River in Mississippi, and *Limonium carolinianum* and *Distichlis spicata* were collected from Deer Island off the coast of Mississippi and from a marsh in Cloud County, Kansas. *Scirpus validus* also was collected from Pascagoula River, Mississippi, and from marshes near St. George, Kansas, and in Decatur County, Kansas. *Spartina alterniflora* plants were from a marsh associated with Davis Bayou in Mississippi.

Plant materials were thoroughly washed and then oven dried at 110°C. Whole plants were separated into aboveground parts, rhizomes, and roots. All plant materials were ground in a Wiley mill before analysis.

Ash and silica contents of plant materials were determined by classical gravimetric techniques. Tissue samples were ashed in platinum crucibles at approximately 500°C, and the ash was treated repeatedly with 6N hydrochloric acid to remove other mineral impurities. The silica was filtered out and ignited. Silicon dioxide content of plant materials was determined as the difference in weights before and after treatment in a platinum crucible with a few drops of 45% aqueous hydrofluoric acid (Kolthoff and Sandell 1952). Determinations were made in duplicate.

The X-ray diffraction patterns for identifying the nature of the mineral deposits in the plants were made as described by Lanning et al. (1958).

Scanning electron micrographs of mineral deposits in leaves of the plants were made with an ETEC Autoscan E-1 Electron Microscope. Tissues were ashed between microscope slides as described below. Ash was transferred to an aluminum stub covered with double-faced sticky tape by lightly pressing the stub on the glass slide; then the ash was coated with Au-Pd alloy and carbon. In some cases, tissue was ashed in a small platinum crucible and treated with 6N HCl to remove soluble minerals before it was mounted on the stub.

Spodograms were prepared by the Ponnaiya (1951) modification of the Uber (1940) method. Material to be examined was placed between microscope slides for ashing in a muffle furnace at 500°C. Ash was prepared for light microscopy by removing the upper slide, adding Canada balsam directly to the ash, and covering with a cover glass. A petrographic microscope was used to determine the nature of silica in the deposits.

RESULTS

Ash and Silica Contents of Plant Tissues

Petrographic microscope studies of plants other than *Limonium carolinianum* showed silica to be clear, colorless, and isotropic with an index of refraction of 1.45. These are properties of the mineral opal (Lanning et al. 1958). Silica content of *Limonium carolinianum* was quite low, and both petrographic microscope studies and X-ray diffraction patterns showed the presence of α-quartz. Silica in *L. carolinianum* was probably detrital quartz. There also was some detrital quartz in *Scirpus validus* leaves.

The ash and silica contents of the tissues of the plants analyzed are given in Tables 1 and 2. Ash content of *Limonium carolinianum* leaves was very high, and low silica content indicated an unusual mineral content. X-ray diffraction patterns of the ash of leaves showed a large amount of halite (sodium chloride) and a calcium sodium phosphate (2.4 CaO · 0.6 Na_2O · P_2O_5). Ando (1958) prepared this substance by fusing CaC_2O_4 with Na_2CO_3 and H_3PO_4 for 1/2 an hour at 1,300°C, and determined its X-ray diffraction pattern to be an α-rhenanite structure. X-ray diffraction of leaves also showed the halite. Other peaks were too small for positive identification but indicated that calcium sodium phosphate was present in the leaves of *Limonium carolinianum*. X-ray diffraction also showed the presence of considerable halite and calcium sodium phosphate in the ash of *Spartina alterniflora, Distichlis spicata,* and *Scirpus validus* leaves of plants from Mississippi. However, halite was not present in *Zizania aquatica.*

Minerals tend to deposit in leaves as shown by both higher ash and silica contents. *Limonium carolinianum* differs from other plants in that it does not accumulate silica in any great amount. *Zizania aquatica* leaves have the highest silica content of any of the plant parts tested, and silica makes up half of the ash. The nodes of the culms of *Zizania*

TABLE 1.

Percentage of Ash in Marsh Plants.

Plant	Leaves	Rhizomes	Roots	Inflo-rescence	Culm	Culm Nodes
Scirpus validus St. George, Kansas	17.88			7.31		
Scirpus validus Mississippi	17.86	8.33	17.85			
Limonium carolinianum Mississippi	17.11		4.70			
Spartina alterniflora Mississippi	11.95	8.45	15.76			
Zizania aquatica Mississippi	11.71				8.88	13.72
Scirpus validus Decatur County, Kansas	10.65			5.43		
Distichlis spicata Cloud County, Kansas	10.24			9.31		
Distichlis spicata Mississippi	8.18	5.92	19.48			

TABLE 2.

Percentage of Silica in Marsh Plants.

Plant	Leaves	Rhizomes	Roots	Inflo-rescence	Culm	Culm Nodes
Scirpus validus St. George, Kansas	3.39			3.66		
Scirpus validus Mississippi	2.34	1.50	7.02			
Limonium carolinianum Mississippi	0.44		0.14			
Spartina alterniflora Mississippi	0.83	0.95	1.63			
Zizania aquatica Mississippi	6.00				2.04	5.21
Scirpus validus Decatur County, Kansas	1.39			2.49		
Distichlis spicata Cloud County, Kansas	4.55			4.24		
Distichlis spicata Mississippi	2.07	0.21	2.77			

aquatica also have a high silica content. The ash and silica values for *Spartina alterniflora, Distichlis spicata,* and *Scirpus validus* roots are all very high. Although silica content of roots is generally high, some inaccuracy may exist because of residual soil particles. Soil is difficult to wash from roots; therefore, the samples may not have been thoroughly cleaned, thus the very high values.

Scirpus validus plants grown at St. George, Kansas, had considerably more silica in the leaves than those from Mississippi, and the latter had considerably more than those from Decatur County, Kansas. *Distichlis spicata* leaves from Cloud County, Kansas, had twice as much silica as those from Mississippi. Inflorescences of Kansas plants had nearly as much or somewhat more silica than the leaves; silica in each inflorescence made up almost half of the ash.

Patterns of Ash and Silica Depositions

Electron micrographs of mineral deposition in ashed leaf tissue of *Zizania aquatica* leaves are shown in Figure 1. The deposits are in rows lengthwise of the leaves. Figure 1A shows rows of solid deposition, a row of "bowtie" phytoliths, and a row of the bowtie phytoliths joined together at the sides. Also there are oval phytoliths and open spaces that appear to be stomata. These are shown highly magnified in Figure 1B. The bowtie-shaped phytoliths are shown in Figure 1C, and the bowtie phytoliths joined together in Figure 1D.

Petrographic microscope examination of silica deposits in *Zizania aquatica* leaves shows that they occur in bowtie-shaped particles. Silica also occurs in cell walls. These silica deposits in cell walls run in strips lengthwise of the leaves, and form bands three cells wide.

Figure 2A is an electron micrograph of mineral deposition in ashed leaf tissue of *Distichlis spicata* leaves. Mineral deposits occur in rows of elongate, serrated units with the longer dimension lengthwise of the leaf. There are also some small rectangular particles and some irregular oval particles. Examination of acid-treated deposits with a light microscope shows silica deposition to be in rows of elongate units, and it appears to be in cell walls.
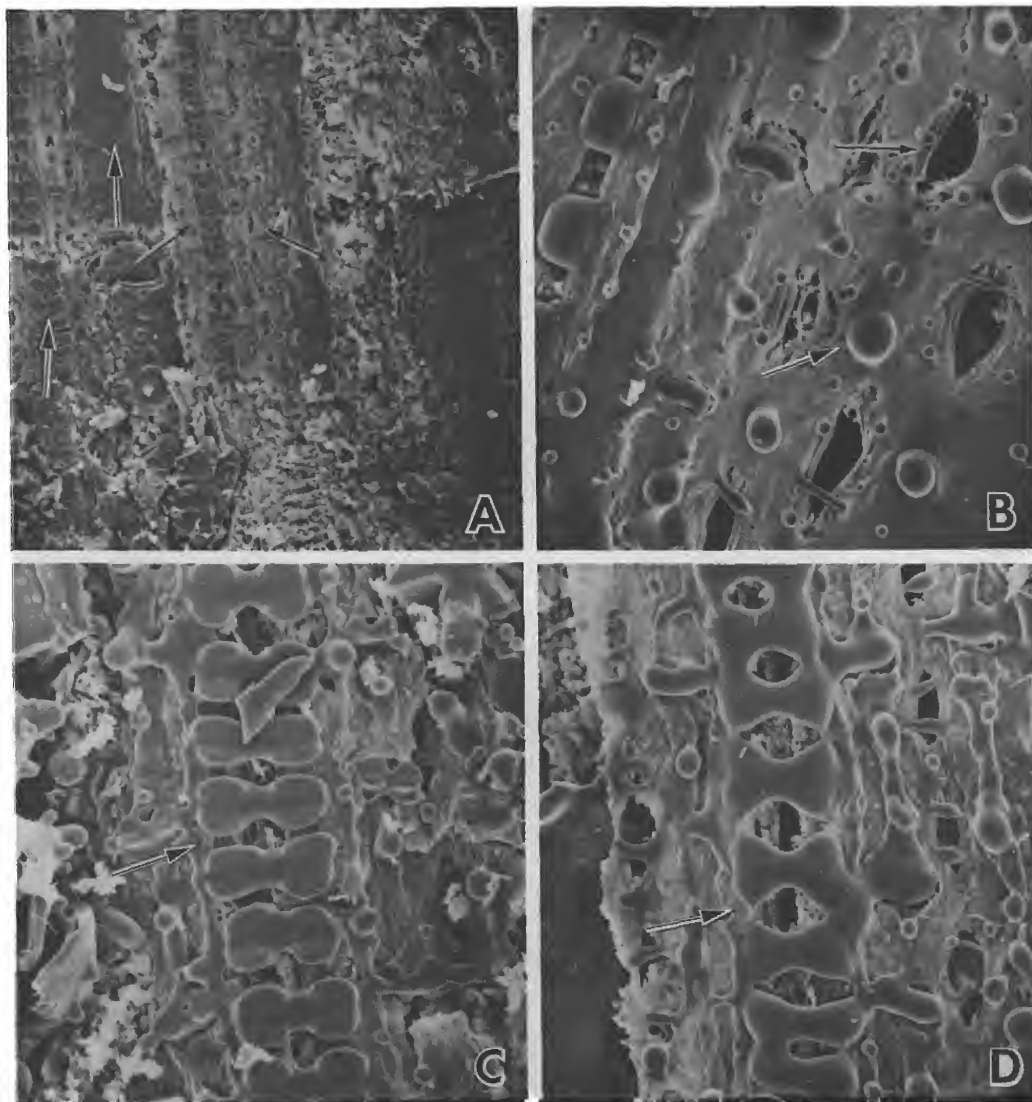
Figure 1. Scanning electron micrographs of ash deposits in *Zizania aquatica* leaves. A. Leaf surface showing all types of mineral deposition including rows of solid deposition (large arrowhead), a row of bowtie-shaped phytoliths (large arrow), a row that appears to be bowtie-shaped phytoliths joined together at the sides (small arrow), oval phytoliths (small arrowhead), and open spaces that appear to be stomata (small long arrow). $\times$ 250. B. A portion of leaf tissue with oval particles (arrowhead) and stomata (small arrow). $\times$ 1000. C. A portion of leaf showing the row of bowtie-shaped phytoliths (large arrow). $\times$ 1000. D. A portion of leaf showing the row of bowtie-shaped phytoliths joined together (large arrow). $\times$ 1000.

Heavy deposits of minerals occur in ridges lengthwise in *Spartina alterniflora* leaves. Ashed leaf tissue with a spongy deposition running continuously lengthwise of the leaf are shown in the electron micrograph of Figure 2B. Figure 2C, another electron micrograph of leaf tissue lengthwise of the leaf, shows a more fibrous character of mineral deposition.

An electron micrograph of acid-treated mineral deposits shows that silica deposition is largely fibrous in character with some irregular particles (Figure 2D).

In *Scirpus validus*, deposits of minerals also occur in ridges lengthwise of the leaf, and rows of oval particles were observed with a light microscope. Silica occurs in a sheetlike
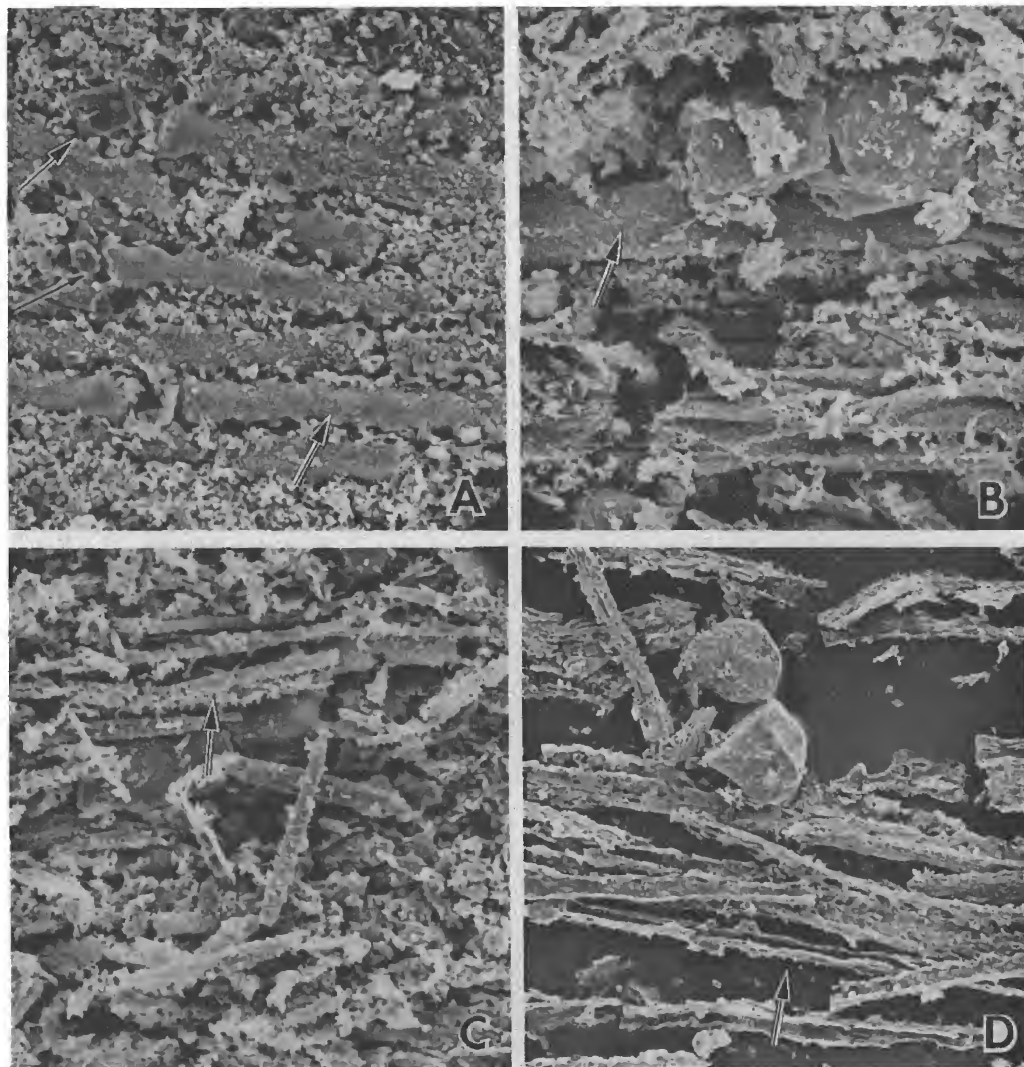
Figure 2. Scanning electron micrographs of ash deposits. A. Leaf surface showing deposits in *Distichlis spicata*. Note the rows of elongate, serrated units lengthwise of the leaf (large arrow), small rectangular particles (arrowhead), and irregular oval particles (small arrow). × 1000. B. Ash deposit from *Spartina alterniflora* leaf. Note the spongy deposition running continuously lengthwise of the leaf (large arrow). × 1000. C. Electron micrograph of *Spartina alterniflora* leaf. Note the fibrous character of mineral deposition (large arrow). × 1000. D. Silica in *Spartina alterniflora* leaf. Specimen was acid washed to remove other minerals. Note the fibrous character of the deposits (large arrow). × 125.

pattern and in rows of oval particles.

Limonium carolinianum leaves do not show a distinct pattern of mineral deposition other than heavier deposits in the veins.

DISCUSSION

Scirpus validus plants grown at St. George, Kansas, had considerably more silica in the leaves than those from Mississippi, and the latter had considerably more than those grown in Decatur County, Kansas. *Distichlis spicata* plants grown in Cloud County, Kansas, had twice as much silica in the leaves as those from Mississippi. These differences may be due to the amount of available silica in soils at the different locations. However, within a species genetic differences (local adaptation) in uptake capability may exist. Resolution of this question may be obtained by growing plants of the same species collected from widely separated localities in a common environment. Jones and Handreck (1965, 1969)

contend that silica uptake is passive, but Barber and Shone (1966) obtained evidence that uptake of silica may be metabolic. Thus, environmental differences may account for variation between species.

Attention should be focused on the fact that wild rice (*Zizania aquatica*), a close relative taxonomically to cultivated rice (*Oryza satina*), had the highest silica content of the plant species studied. This is an interesting discovery since highly bred cultivated rice also has the ability to accumulate large quantities of silica. Furthermore, silica of *Zizania aquatica* is deposited in a very unusual pattern.

Spartina alterniflora had a relatively low silica content. Although this plant is often found with the lower portion submerged in water and is generally found on muddy shores, the collections analyzed in this study were from a very sandy area. The rectangular silica deposits in the leaf ridges of *Spartina alterniflora* may aid in reducing transpiration. Transpiration presumably is lowered by increasing thickness and compactness of silica cellulose membranes in the epidermal cells (Yoshida et al. 1959). Leaves of *Spartina alterniflora* during periods of very high temperatures become rolled. Rectangular silica deposits also occur in *Distichlis spicata* linking these two grass species. The bowtie-or dumbbell-shaped silica deposits in *Zizania aquatica* are an entirely new type of structure, with no parallel in cultivated rice.

The low silica content of *Limonium carolinianum*, a dicotyledon, is consistent with previous evidence in that the monocotyledon analyzed had consistently higher silica contents.

This preliminary study on grasses, sedges, and a dicot species, and previous work on the rush *Juncus roemerianus*, suggests that at least some of the information determined for cultivated plants also holds true for wetland species. However, each of the species investigated had peculiar depositional characteristics and various quantities of silica. Further study of wetland species is needed before there can be any clear understanding or definite statements relating our work to the agriculture literature and to that pertaining to upland species.

In closing, we point out that the continued release of domestic sewage into estuarine waters is very likely to raise the nitrogen and phosphorous concentrations of wetlands soils. High nitrogen and phosphorous concentrations are known to decrease silica content of domestic plants as shown above with corresponding detrimental effects: weakened plants, reduced photosynthesis, and increased fungal and insect attacks. In view of these facts and possibilities, it is timely and prudent to carry out work that would lead to a better understanding of the role of silica in wetland and aquatic plant species.

ACKNOWLEDGMENTS

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January 1981

Pseudomma heardi, a New Peracarid (Crustacea: Mysidacea) from Continental Shelf Waters Off Mississippi

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PSEUDOMMA HEARDI, A NEW PERACARID (CRUSTACEA: MYSIDACEA) FROM CONTINENTAL SHELF WATERS OFF MISSISSIPPI

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ABSTRACT   *Pseudomma heardi* n. sp. is described and illustrated. Specimens were obtained from plankton samples taken in 18 to 60 meters depth in offshore waters of Mississippi. This new species can be distinguished from other species of *Pseudomma* by the presence of 16 to 21 serrations on the anterior and lateral margins of the ocular plate, strong lateral spine of antennal scale which extends well beyond apex of scale and 4 to 6 spines on lateral margins of telson.

INTRODUCTION

The offshore mysid fauna of the Gulf of Mexico is poorly known. While approximately 28 species of mysids have been reported from Gulf waters (Tattersall 1951; Brattegard 1969, 1970; Stuck et al. 1979a; Stuck and Heard 1981), the majority are known only from estuarine and nearshore waters. Examination of plankton samples taken in offshore waters of Mississippi revealed the presence of an undescribed species of mysid referable to the genus *Pseudomma* Sars, 1879.

Stuck et al. (1979a) first recorded the occurrence of the present species of *Pseudomma* from eastern Gulf of Mexico waters. A brief description of the female (Stuck et al. 1979b) was presented; however, a complete description awaited the collection of male specimens.

Sars (1870) erected the genus *Pseudomma* within the tribe Erythropini to include two species, *P. affine* Sars, 1870 and *P. roseum* Sars, 1870. Murano (1974) reviewed the genus, described 11 new species from the central and western Pacific and provided a key for the identification of 34 species. *Pseudomma californica* Băcescu and Gleye, 1979 has since been described from California waters (Băcescu and Gleye 1979). With the addition of the present material, the genus now contains 36 species. All species of *Pseudomma* are easily distinguished from other species of Erythropini by the possession of a large ocular plate formed by the fused eyestalks which lacks a prominent spinous process on its anterolateral margin.

MATERIALS AND METHODS

Specimens used in the present study were obtained from plankton samples collected from continental shelf waters off Mississippi through a National Marine Fisheries Service grant, Public Law 88–309, Project 2–42–R. Samples were obtained using a 0.5 m plankton net with 0.5 mm mesh netting and equipped with flow meter and opening-closing device. Simultaneous surface, midwater, and bottom samples were taken at each sampling site. Measurements of total length were made from the anterior margin of the

rostral plate to the distal tip of the telson. The holotype and one paratype specimen were deposited in the United States National Museum of Natural History (USNM), Washington, D.C. Additional paratype material has been deposited in the museum of the Gulf Coast Research Laboratory, Ocean Springs, Mississippi.

TAXONOMIC DESCRIPTION

Pseudomma heardi new species

Pseudomma sp., Stuck et al. 1979b: p. 233, figs. 2e, 3e, 4e, 5e

Material Examined — 2 males (3,8 mm, 3.7 mm); 30°02′30″N, 88°40′15″W; bottom water plankton tow; depth 18 meters; 11-20-68. 1 female (3,8 mm); 29°42′00″N, 88°27′30″W; midwater plankton tow; depth 37 meters; 11-12-68. 2 females (3.5 mm, 3.7 mm); 29°24 15″N, 88°17′00″W; bottom water plankton tow; depth 60 meters; 11-20-68.

Diagnosis — Lateral tooth of antennal scale extending well beyond apex. Anterior and lateral margins of ocular plate with 16 to 21 coarse teeth. Terminal segment of endopod of male fourth pleopod without single long modified seta. Endopods of uropods extending well beyond distal tip of telson, slightly shorter than exopods. Lateral margin of telson with 4 to 6 spine-like serrations, apex armed with 3 pairs of long spines increasing in length medially.

Description

General body form (Figure 1) — slender, small, adult males and females to 3.8 mm; thorax and abdomen distinctly separate.

Anterior margin of carapace evenly convex, anterolateral corners rounded; dorsal gastric region just anterior to cervical sulcus swollen in appearance; posterior margin emarginate, exposing eighth thoracic segment.

Frontal lamina (Figure 2A) — scarcely visible below ocular plate in dorsal view, anterior margin armed with about 13 dorsally pointed serrations.

Antennular peduncle (Figure 2B) — more robust in males than females, first segment twice length of second, slightly
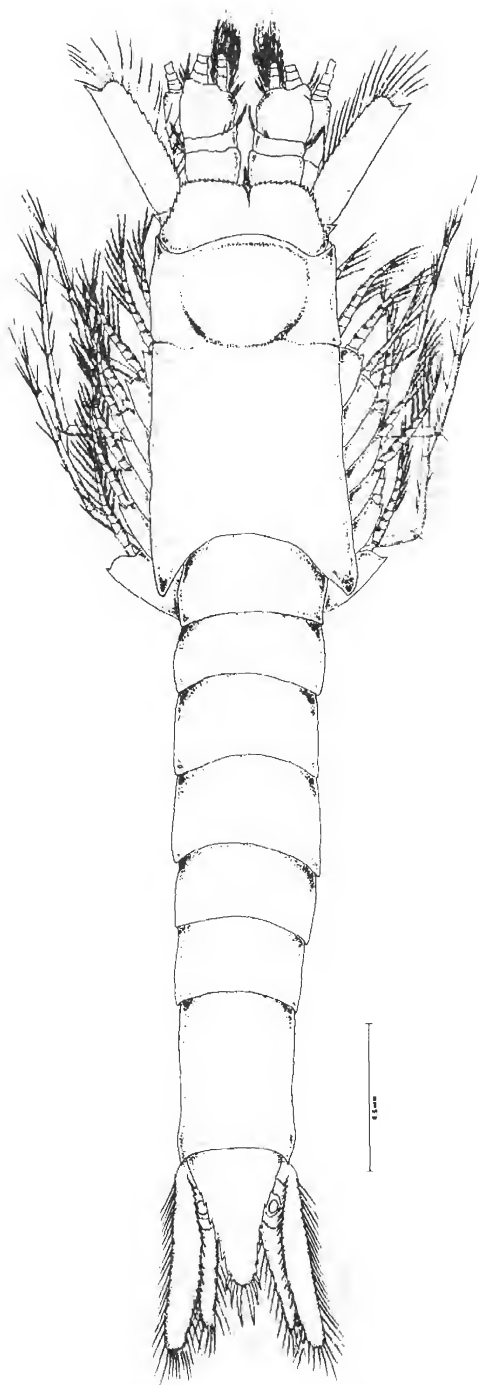
Figure 1. Entire body, dorsal (3.7 mm male).

shorter than third; distolateral margin of first segment somewhat produced, bearing pair of large plumose setae and pair of smaller simple setae; distomedial margin of second segment bearing pair of large plumose setae and several simple setae; distolateral margin of third segment with few simple setae, distomedial margin with 1 or 2 plumose setae and pair of simple setae, males with densely setose lobe on ventral margin; flagellum typical of genus.

Antennal scale (Figure 2C) — about 3.8 times as long as maximum width, lateral margin straight, devoid of setae, ending in strong lateral tooth which extends well beyond apex, inner margin and apex setose; second and third segments of peduncle subequal in length, distomedial margin of third segment bearing cluster of simple setae, outer margin with single simple seta, second segment with pair of stout plumose setae and single long simple seta on distomedial margin; first segment very small, barely distinguishable from sympod; flagellum typical of genus.

Eyestalks fused into large rectangular ocular plate, cleft in midline, anterior and lateral margins armed with 16 to 21 coarse teeth.

Mandible (Figure 2D) — typical of genus; palp with enlarged second segment, bearing row of about 8 plumose setae on inner margin, outer margin with about 12 long simple setae and several plumose setae; third segment about 0.6 times as long as second, reduced in width, bearing row of about 18 pectinate setae on posterior margin and a single long barbed, curved spine distally.

Maxillule (Figure 2E) — typical of genus; inner lobe with 3 large spined "setae" and several smaller simple and plumose setae; outer lobe with about 10 stout, serrate apical spines and cluster of 3 plumose subapical setae.

Maxilla (Figure 2F) — typical of genus, exopod large, bearing about 11 plumose setae along outer margin; endopod 2-segmented, bearing about 15 long plumose setae on apex and inner margin; third sympodal segment trilobed, bearing numerous serrate spines and plumose setae; lobe of second sympodal segment enlarged, bearing about 25 long plumose setae on distal margin.

Endopod of first thoracic limb (Figure 3A) — robust, dactyl bearing strong simple spine on distal tip, posterior margin bearing two strong serrate "setae," anterior margin with cluster of 4 plumose setae; carpo-propodus subequal in length with merus and ischium, bearing cluster of 3 plumose setae and single simple seta on posterior distal corner, one plumose seta on anterior margin; posterior margins of merus, ischium and preischium with 8, 7, and 5 stout plumose setae, respectively, decreasing in length proximally, anterior margins of each segment with single plumose seta; posterior margin of basis pubescent, bearing pair of plumose setae on inner, lateral, and distal margins.

Endopod of second thoracic leg (Figure 3B) — stout; dactyl one-half length of carpo-propodus, with strong simple spine on distal tip, anterior margin bearing 5 plumose "spines" and single simple seta, posterior margin with
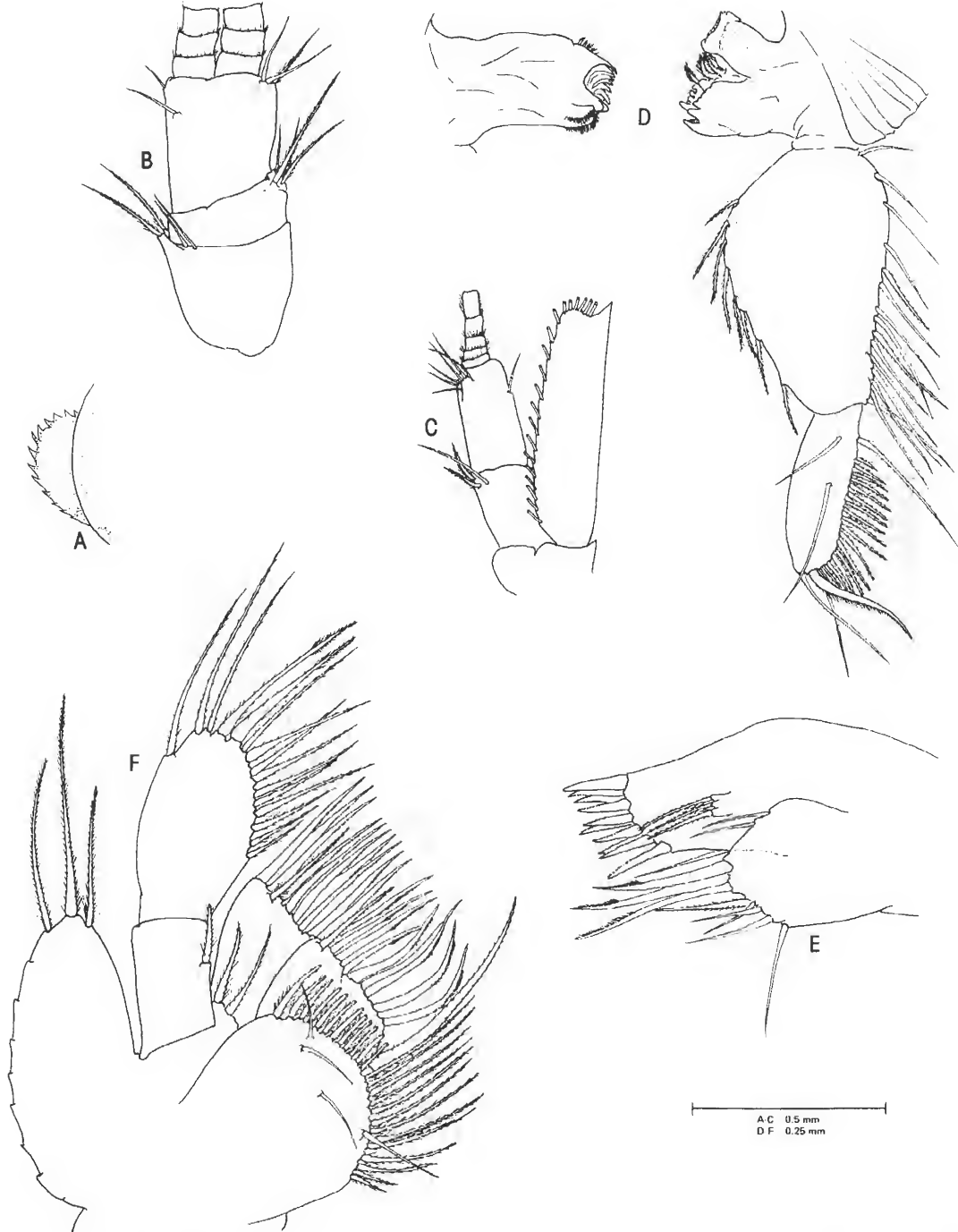
Figure 2. A. Frontal lamina (lateral view); B. Antennular peduncle; C. Antennal peduncle and scale; D. Left and right mandible with palp; E. Maxillule; F. Maxilla. A, E–F. 3.7 mm male; B, C. 3.7 mm female.
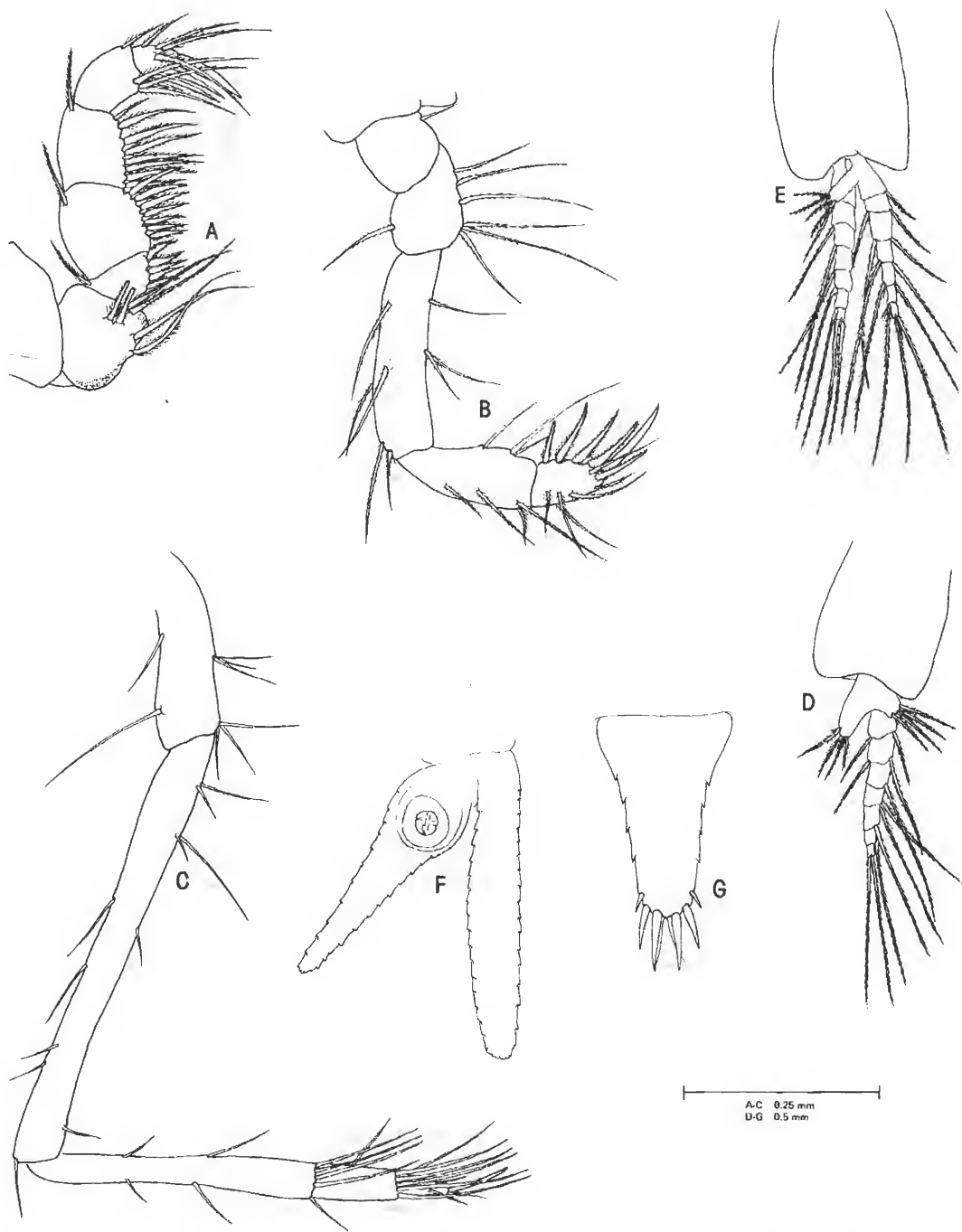
Figure 3. A. Endopod, first thoracic leg; B. Endopod, second thoracic leg; C. Endopod, third thoracic leg; D. First pleopod; E. Fourth pleopod; F. Right uropods; G. Telson. A–E. 3.7 mm male; F, G. 3.7 mm female.

plumose setae; merus slightly longer than carpo-propodus, twice length of ischium.

Endopod of third thoracic leg (Figure 3C) – slender; dactyl bearing simple spine on distal tip, partially obscured by dense cluster of simple and plumose setae extending from distal margin of propodus; distal margin of carpus also with cluster of simple setae; anterior margins of ischium, merus, and carpus with scattered clusters of simple setae.

First male pleopod (Figure 3D) – with 1-segmented endopod bearing 4 plumose setae distally and pseudo-branchial lobe furnished with 4 plumose setae, exopod 7-segmented.

Fourth male pleopod (Figure 3E) – with 7-segmented endopod bearing pseudobranchial lobe similar to first pleopod; lacking extremely long simple seta on terminal segment; exopod 7-segmented.

All pleopods of female reduced to simple setose, uniramous plates.

Uropods (Figure 3F) – slender, exopod about 1.25 times as long as endopod, 1.6 times as long as telson; exopods and endopods devoid of spines, setose along both inner and outer margins.

Telson (Figure 3G)   linguiform, shorter than sixth abdominal segment, apex armed with 3 pairs of spines increasing in length medially and a pair of delicate plumose setae, apical spines longer in males than females, lateral margins slightly concave, bearing 4 to 6 "serrations."

Holotype – USNM 181984, male (3.8 mm); 30°02'30"N; 88°40'15"W.

Paratype – USNM 181985, female (3.8 mm); 29°42'00"N; 88°27'30"W.

Type habitat – Mid- and bottom-water plankton in 18 to 60 meters depth, continental shelf waters off Mississippi coast.

Etymology – This species is named in honor of Richard Heard in recognition of his work on Crustacea of the northern Gulf of Mexico.

Remarks

Pseudomma heardi n. sp. appears to fit best into the *Affine* species group (sensu Murano 1974). This group is characterized by serrate eyeplates and telsons with 3 to 6 lateral and 3 or 4 pairs of apical spines. Certain peculiarities should, however, be noted in the present species. A vertically descending serrated frontal lamina beneath the ocular plate as illustrated here has not been noted in other species of the genus. The lateral margins of the telson in all specimens examined did not bear distinct spines, but rather appeared serrate as in *P. crassidentatum* Murano (1974, Fig. 18e).

The following combination of characters best distinguish *P. heardi* from the other described species of *Pseudomma*:

1. Ocular plate with 16 to 21 teeth on the anterior and lateral margins.

2. Lateral tooth of antennal scale extending well beyond apex.

3. Pleopods of male with endopods and exopods subequal in length and not bearing long specialized setae on terminal segments.

4. Telson with 4 to 6 serrations on lateral margins and 6 apical spines.

Pseudomma heardi is the first species of *Pseudomma* reported from Gulf of Mexico waters. Three species, *P. truncatum*, *P. affine*, and *P. roseum*, have been reported from the western North Atlantic (Tattersall 1951).

Murano (1974) has described the habitat of the genus *Pseudomma* as living on or close to the seafloor, having taken most species by bottom-water plankton nets and from the stomachs of benthic fishes. Wigley and Burns (1971) reported *P. affine* from benthic samples taken from the Gulf of Maine and south of Georges Bank. They reported the bathymetric range of all records from the North Atlantic as 80 to 914 meters. While very few specimens of *P. heardi* were obtained, all were taken from bottom and midwater plankton samples in relatively deep shelf waters.

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Gulf Research Reports

Trends in Ex-Vessel Value and Size Composition of Reported May - August Catches of Brown Shrimp and White Shrimp from the Texas, Louisiana, Mississippi, and Alabama Coasts, 1960-1978

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TRENDS IN EX-VESSEL VALUE AND SIZE COMPOSITION OF REPORTED MAY–AUGUST CATCHES OF BROWN SHRIMP AND WHITE SHRIMP FROM THE TEXAS, LOUISIANA, MISSISSIPPI, AND ALABAMA COASTS, 1960–1978[1]

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ABSTRACT   Exponential models were used to characterize (1) ex-vessel value (in dollars) per shrimp by size category (count; i.e., number of shrimp per pound, heads off); (2) size composition (expressed as cumulative weight of the catch in pounds, heads off, by size category); and (3) ex-vessel value composition (expressed as cumulative ex-vessel value, in dollars, of the catch by size category) for reported May–August catches (inshore and offshore combined) of brown shrimp (*Penaeus aztecus*) and white shrimp (*P. setiferus*) from the Texas, Louisiana, Mississippi, and Alabama coasts (statistical areas 10–21) from 1960 to 1978. Exponents of the models were used as indices to investigate trends in ex-vessel value per shrimp, size composition, and ex-vessel value composition of the May–August catches during this period. This approach to analysis of catch statistics can be used to monitor these fisheries, and the results can be compared with changes that may be brought about by the closure of the fishery conservation zone off Texas, as proposed by 1981 by the Gulf of Mexico Fishery Management Council, in the fishery management plan for the shrimp fishery of the Gulf of Mexico.

INTRODUCTION

The fishery management plan for the shrimp fishery of the Gulf of Mexico, prepared by the Gulf of Mexico Fishery Management Council (GMFMC 1980), proposed a simultaneous closing of the territorial sea of the State of Texas and the adjacent fishery conservation zone (FCZ) to shrimping during the time of the year when brown shrimp (*Penaeus aztecus*) in these waters are, for the most part, smaller than 65 count (refers throughout this paper to number of shrimp per pound, heads removed). The territorial sea is the area under state jurisdiction extending from the coastal baseline to 9 nautical miles off Texas (Figure 1). The FCZ is the area under federal jurisdiction beginning at the outer limit of Texas' territorial sea and extending 200 miles from shore. The closing of Texas' territorial sea to shrimping normally begins June 1 and extends to July 15. However, a 15-day flexibility in the closing and opening dates is allowed to accommodate effects of climatic variations on shrimp growth, within the restriction that the period of closure does not exceed 60 days. The inclusive dates for the closure in 1981 were May 22–July 15. The management plan encouraged the State of Texas to continue its seasonal closure of the territorial sea, to eliminate minimum size restrictions on shrimp caught in open waters before and after the closure, and to evaluate the effect of allowing white shrimp (*P. setiferus*) fishing to continue within the closed areas during the closure.

Rationale for the proposed closure was an expected increase in yield from additional growth of the protected brown shrimp, and from the elimination of waste due to discarding of undersized brown shrimp in the FCZ

(GMFMC 1980). The management plan recognized that the closure might affect other fishing areas (e.g., the coasts of Louisiana, Mississippi, and Alabama) by shifting fishing effort to those areas. Therefore, it was the intent of the management plan that the biological, ecological, social and economic impacts of the closure be monitored in 1981 so that revisions could be made if warranted.
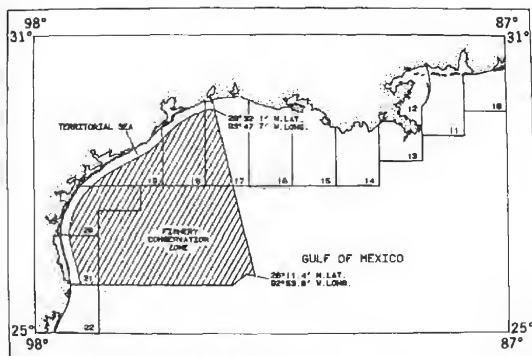
Figure 1. Boundaries of statistical areas 10–21, the Texas territorial sea, and the fisheries conservation zone off Texas (based on information from GMFMC 1980).

As might be expected, the proposed closure of the FCZ off Texas has become a highly controversial issue. There is considerable interest and concern on the part of the fishing industry, the Gulf states, the GMFMC, the National Marine Fisheries Service (NMFS), and fishery scientists regarding the potential impacts of the proposed closure.

We expect that the redistribution of fishing effort, the changes in fishing strategy, and the additional shrimp growth that may result from the closure will cause changes in size composition of the combined inshore and offshore catch.

Inshore waters generally are considered to be landward of the barrier islands, and are represented by bays or estuaries. Offshore waters are seaward of the barrier islands. According to Henderson (1972) and Ricker (1975), an increase in average size of individuals in the catch could indicate a decrease in mortality (usually equated with a decrease in fishing mortality) or an increase in growth (e.g., if recruitment were poor, and if population density were low as a consequence). A decrease in average size might be brought about after the closure by retention and landing of large quantities of small shrimp, previously discarded at sea. Also a decrease in average size might be caused by an intensification of fishing in offshore and inshore waters open to shrimping in other areas during the closure. Socioeconomic factors leading to changes in strategies of fishing, culling of the catch, and marketing of the landings also could influence size composition of the catch.

Caillouet et al. (1980) developed a simple exponential model to characterize the size composition (expressed as cumulative percentage of weight of catch by size category) of annual catches of shrimp. They showed that the size of brown and white shrimp in the reported annual catches from Texas and Louisiana decreased from 1959 to 1976. Caillouet and Koi (1980) modified the model by applying it to cumulative weight by size category instead of cumulative percentage of weight by size category, and used it to investigate trends in size composition of the annual landings of brown, pink (*P. duorarum*), and white shrimp from the Gulf and southeast coast fisheries of the United States from 1961 to 1977. Caillouet and Koi (1980) also used exponential models to investigate trends in ex-vessel value per shrimp by size category, size composition, and ex-vessel value composition of these annual landings. Using the methods of Caillouet and Koi (1980), Caillouet and Koi (1981) investigated trends in ex-vessel value per shrimp by size category, size composition, and ex-vessel value composition of reported annual catches of pink shrimp from the Tortugas fishery off south Florida from 1960 to 1978. The effect of shrimp size on the ex-vessel value of the catch has also been recognized by Neal (1967), Griffin et al. (1974), Griffin and Nichols (1976), and Griffin et al. (1976).

The NMFS has the responsibility for monitoring impacts of closing the FCZ off Texas. The purposes of this paper are to propose a procedure for monitoring the brown and white shrimp fisheries of Texas, Louisiana, Mississippi, and Alabama, based on the methods of Caillouet and Koi (1980), and to use these methods to investigate trends in ex-vessel value per shrimp by size category, size composition and ex-vessel value composition of the reported May—August catches from 1960 to 1978. This approach can then be used as one means of assessing the impacts of closing the FCZ off Texas in 1981. The period May-August was chosen for these analyses to assure that the period of closure of Texas' territorial sea and the FCZ would be encompassed, considering the allowed flexibility in the starting and ending dates for the closure. Including May and August in the time interval of coverage for the years 1960–1978 will assure that some catch statistics will be available from the Texas coast for future comparison with those from Louisiana, Mississippi, and Alabama for the May-August period in 1981.

DESCRIPTION OF DATA

Summaries of the May—August catches of brown and white shrimp and their ex-vessel value were compiled from data files available from the NMFS, Southeast Fisheries Center (SEFC) Technical and Information Management Services (TIMS), Miami, Florida. The combined weight of the reported May-August catches (inshore and offshore combined) was expressed in pounds (heads off) and the ex-vessel value in dollars, by year (1960–1978); coastal area (statistical areas 10-12, 13–17, and 18–21, Figure 1); species (brown and white shrimp); and size category (< 15, 15–20, 21–25, 26–30, 31–40, 41–50, 51–67, and ≥ 68 count, and "pieces," representing parts of shrimp tails that could not be assigned to a count category). Comparable data for the years 1979 through 1981 were not available at the time of this writing.

The three coastal areas are defined as (1) Texas coast (statistical areas 18–21 combined); (2) Mississippi River to Texas (statistical areas 13–17 combined), representing that part of the Louisiana coast west of the Mississippi River; and (3) Pensacola to the Mississippi River (statistical areas 10–12 combined), representing that part of the Louisiana coast east of the Mississippi River, the Mississippi coast, the Alabama coast, and a small part of the upper coast of Florida (catches from Pensacola Bay are not included in this area; they are allocated to the adjacent Apalachicola area by TIMS). Note that part of statistical area 17 is included in the area that was closed in 1981 (Figure 1). Therefore, for the years 1960 to 1978, the May—August catch statistics for the Mississippi River to Texas coastal area represent a somewhat larger zone open to shrimping than was the case in 1981, as a result of the closure. This should be considered in any future analyses applying our methods to data for the Mississippi River to Texas coastal area.

English rather than metric units are used throughout our paper because they have been used historically, and information would have been lost in their conversion to metric units. Catches used herein represent those portions of the actual catches that were landed by domestic commercial fishermen at domestic ports and reported by the National Marine Fisheries Service or its predecessor, the Bureau of Commercial Fisheries, U.S. Fish and Wildlife Service.

ANALYSES AND RESULTS

May—August Catches by Year

The general trends in reported May—August catches, and

their ex-vessel value for both species and the three coastal areas are shown in Figures 2 through 7. In each coastal area, the catch of brown shrimp exceeded that of white shrimp. The general trends in catch were upward, except for white shrimp from Pensacola to the Mississippi River (Figure 7) for which the trend was downward. In all cases, the general trend in ex-vessel value of the catch was upward, but this was not adjusted to account for inflation.

May—August Ex-vessel Value per Shrimp by Size Category

We calculated the May—August average ex-vessel value per shrimp, V, by size category, C, for each year, according to the methods of Caillouet and Koi(1980, 1981), to obtain the following exponential model which described the

relationship between V_i and C_i for each species, coastal area, and year:

$$\hat{V}_i = a \, (\exp bC_i) \qquad (1)$$

where V_i = May—August average ex-vessel value per shrimp for the ith size category; C_i = lower limit (count) of the ith size category ($C_1 = 15, C_2 = 21, C_3 = 26, C_4 = 31, C_5 = 41, C_6 = 51$, and $C_7 = 68$); and i = 1, 2, . . . , 7. The logarithmic form of model 1 was used to estimate parameters a and b by linear regression (Tables 1 through 3). The very high coefficients of determination, r^2, indicated that the straight lines fitted the data very well. All slopes, b, were negative, showing that the value per

Figure 2. Weight (millions of pounds, heads off) and ex-vessel value (millions of dollars) of reported May—August catches (inshore and offshore combined) of brown shrimp from the Texas coast (statistical areas 18–21 combined), 1960–1978.

Figure 4. Weight (millions of pounds, heads off) and ex-vessel value (millions of dollars) of reported May—August catches (inshore and offshore combined) of brown shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1960–1978.

Figure 3. Weight (millions of pounds, heads off) and ex-vessel value (millions of dollars) of reported May—August catches (inshore and offshore combined) of white shrimp from the Texas coast (statistical areas 18–21 combined), 1960–1978.

Figure 5. Weight (millions of pounds, heads off) and ex-vessel value (millions of dollars) of reported May—August catches (inshore and offshore combined) of white shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1960–1978.

Figure 6. Weight (millions of pounds, heads off) and ex-vessel value (millions of dollars) of reported May–August catches (inshore and offshore combined) of brown shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), 1960–1978.
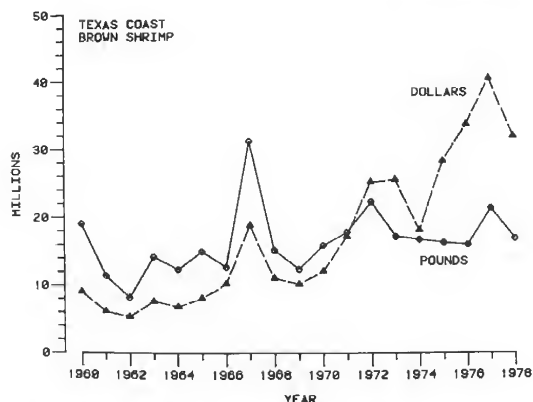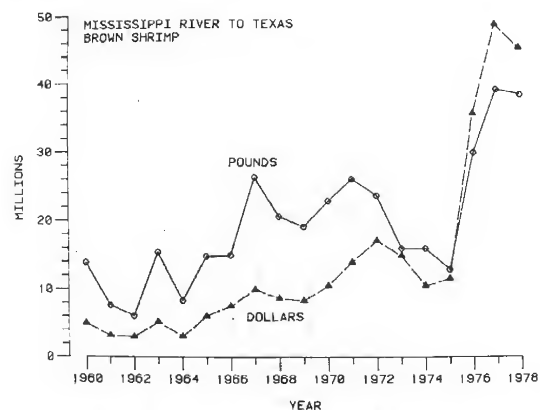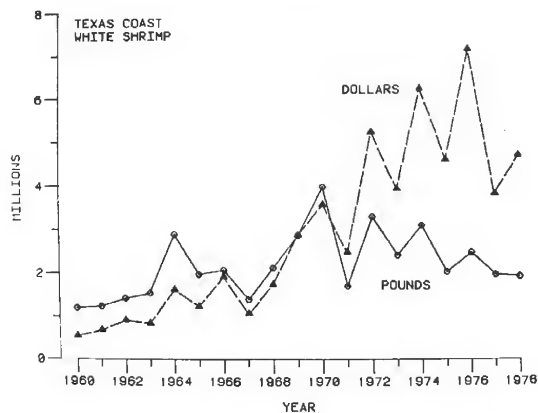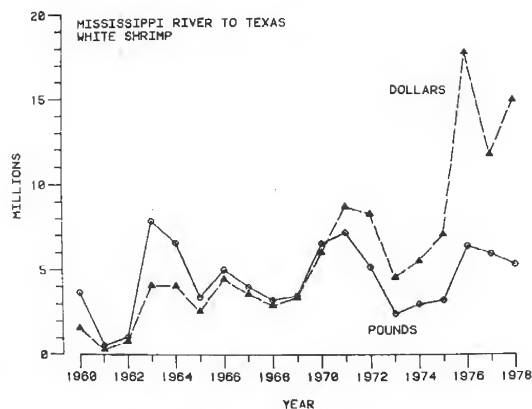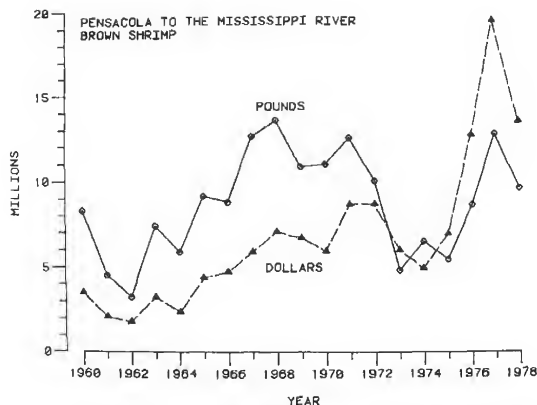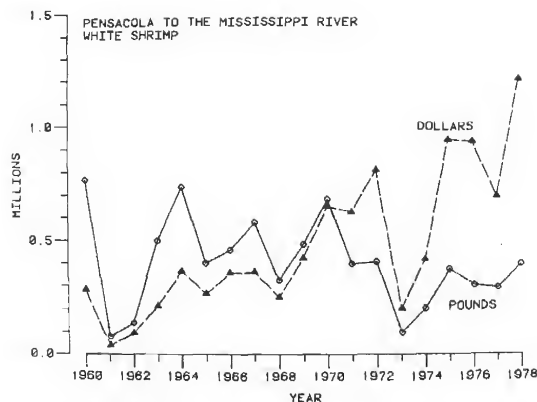

Figure 7. Weight (millions of pounds, heads off) and ex-vessel value (millions of dollars) of reported May–August catches (inshore and offshore combined) of white shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), 1960–1978.

TABLE 1.

Relationship between transformed ex-vessel value (dollars) per shrimp, lnV, and count, C, for reported May-August catches (inshore and offshore combined) of brown and white shrimp from the Texas coast (statistical areas 18–21 combined), 1960–1978.*

Year	Brown Shrimp			White Shrimp		
	a	b	r^2	a	b	r^2
1960	0.07492	−0.04629	0.966	0.07379	−0.04900	0.939
1961	0.08534	−0.04876	0.992	0.07594	−0.04376	0.992
1962	0.12142	−0.04926	0.994	0.11820	−0.05124	0.985
1963	0.11596	−0.05782	0.987	0.09864	−0.05236	0.957
1964	0.09822	−0.05076	0.985	0.09053	−0.04974	0.980
1965	0.11088	−0.05347	0.989	0.09313	−0.04807	0.982
1966	0.15149	−0.05204	0.986	0.12842	−0.04775	0.993
1967	0.11772	−0.05380	0.981	0.11758	−0.05076	0.957
1968	0.16950	−0.05686	0.983	0.12651	−0.04732	0.926
1969	0.18600	−0.05580	0.992	0.19635	−0.06037	0.995
1970	0.17010	−0.05730	0.988	0.15597	−0.05546	0.979
1971	0.25218	−0.05918	0.987	0.19029	−0.04982	0.981
1972	0.26745	−0.05896	0.992	0.27621	−0.05965	0.985
1973	0.30651	−0.05136	0.993	0.23322	−0.04344	0.996
1974	0.29912	−0.06135	0.962	0.31702	−0.06005	0.968
1975	0.37610	−0.05334	0.995	0.36948	−0.05330	0.997
1976	0.59955	−0.06131	0.982	0.57544	−0.05680	0.989
1977	0.51261	−0.05869	0.981	0.53091	−0.05931	0.968
1978	0.59723	−0.05899	0.996	0.41271	−0.04753	0.967

*Based on the linear regression of lnV on C, where V = May-August average ex-vessel value per shrimp in each of seven size categories, C = lower limit (count) of each of the seven size categories, ln(a) = intercept, b = slope, and r^2 = coefficient of determination; all slopes, b, were significantly different from 0 at the 99% level of confidence, and the high r^2 values indicated a very good fit of the straight lines to the data points.

TABLE 2.

Relationship between transformed ex-vessel value (dollars) per shrimp, lnV, and count, C, for reported May-August catches (inshore and offshore combined) of brown and white shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1960–1978.*

Year	Brown Shrimp			White Shrimp		
	a	b	r^2	a	b	r^2
1960	0.07177	−0.04518	0.960	0.08062	−0.04922	0.950
1961	0.07807	−0.04540	0.976	0.07230	−0.04069	0.987
1962	0.10589	−0.04496	0.982	0.10262	−0.04317	0.964
1963	0.10710	−0.05525	0.979	0.11971	−0.05634	0.954
1964	0.09336	−0.05032	0.977	0.08392	−0.04693	0.958
1965	0.09448	−0.04770	0.980	0.09079	−0.04550	0.975
1966	0.13860	−0.04983	0.993	0.11432	−0.04402	0.977
1967	0.11373	−0.05142	0.978	0.13192	−0.05004	0.967
1968	0.16711	−0.05673	0.983	0.15812	−0.05335	0.974
1969	0.18027	−0.05456	0.993	0.16861	−0.05167	0.982
1970	0.16396	−0.05586	0.983	0.15779	−0.05146	0.979
1971	0.26244	−0.06079	0.991	0.22663	−0.05676	0.988
1972	0.25174	−0.05603	0.991	0.27206	−0.05543	0.981
1973	0.28208	−0.04830	0.996	0.23883	0.04253	0.991
1974	0.31893	−0.06200	0.963	0.34038	−0.06098	0.953
1975	0.44343	−0.05921	0.998	0.39411	−0.05521	0.997
1976	0.54890	−0.05990	0.990	0.64588	−0.06011	0.992
1977	0.50268	−0.05870	0.979	0.51734	−0.05844	0.971
1978	0.55672	−0.05896	0.998	0.47111	−0.05203	0.990

*Based on the linear regression of lnV on C, where V = May-August average ex-vessel value per shrimp in each of seven size categories, C = lower limit (count) of each of the seven size categories, ln(a) = intercept, b = slope, and r^2 = coefficient of determination; all slopes, b, were significantly different from 0 at the 99% level of confidence, and the high r^2 values indicated a very good fit of the straight lines to the data points.

TABLE 3.

Relationship between transformed ex-vessel value (dollars) per
shrimp, lnV, and count, C, for reported May-August catches
(inshore and offshore combined) of brown and white
shrimp from Pensacola to the Mississippi River
(statistical areas 10–12 combined),
1960–1978.*

Year	Brown Shrimp			White Shrimp		
	a	b	r^2	a	b	r^2
1960	0.06459	−0.04092	0.950	0.07132	−0.04533	0.954
1961	0.06892	−0.04052	0.953	0.06839	−0.03821	0.965
1962	0.09940	−0.04296	0.953	0.09536	−0.04022	0.962
1963	0.08738	−0.04806	0.951	0.09655	−0.05245	0.950
1964	0.08482	−0.04654	0.963	0.08617	−0.04676	0.977
1965	0.08664	−0.04376	0.956	0.08619	−0.04278	0.944
1966	0.12705	−0.04682	0.986	0.11061	−0.04302	0.956
1967	0.09783	−0.04687	0.952	0.12206	−0.05243	0.929
1968	0.15802	−0.05362	0.974	0.14762	−0.05040	0.963
1969	0.16800	−0.05224	0.981	0.14203	−0.04660	0.940
1970	0.14682	−0.05182	0.966	0.14364	−0.05006	0.951
1971	0.24106	−0.05768	0.982	0.21810	−0.05502	0.984
1972	0.23786	−0.05198	0.974	0.03587	0.01917†	0.063†
1973	0.29481	−0.04925	0.991	0.25034	−0.04056	0.995
1974	0.31528	−0.05927	0.968	0.34052	−0.06087	0.943
1975	0.38841	−0.05390	0.996	0.34995	−0.05095	0.987
1976	0.54194	−0.05741	0.980	0.54105	−0.05609	0.966
1977	0.47724	−0.05660	0.967	0.50089	−0.05739	0.977
1978	0.50039	−0.05555	0.995	0.43380	−0.04895	0.987

*Based on the linear regression of lnV on C, where V = May-August
average ex-vessel value per shrimp in each of seven size categories,
C = lower limit (count) of each of the seven size categories, ln(a) =
intercept, b = slope, and r^2 = coefficient of determination; all
slopes, b, except one, were significantly different from 0 at the 99%
level of confidence, and the high r^2 values indicated a very good fit
of the straight lines to the data points.

†The slope, b, for white shrimp in 1972 did not differ significantly
from 0 at the 95% level of confidence, and the r^2 value was very
low, because no catch was reported for the $\geq$ 68 count category.

shrimp decreased with increase in count (decrease in size),
as expected.

Lower limits rather than midpoints or upper limits of
the seven size categories were used in constructing model 1,
as in Caillouet and Koi (1980, 1981). The < 15 category
represented $\leq$ 3% of the May–August catches of brown
shrimp in each of the three coastal areas in any given year.
However, for white shrimp, the < 15 category represented
as high as 23% of the May–August catches from the Texas
coast, 15% from the Mississippi River to Texas, and 28%
from Pensacola to the Mississippi River in certain years. We
did not include the < 15 size category in model 1 to be
consistent with previous work, and because the logarithmic
form of model 1 is not a straight line in the region of < 15
count (Caillouet and Koi 1980, 1981; Caillouet et al. 1980).
The category "pieces" was excluded from the model because
it represented parts of shrimp tails which could not be
assigned to a count category. The constant, a, reflected the
elevation of the straight line which was influenced in part

by our use of lower limits of size categories and exclusion
of the < 15 size category in fitting the model. The slope, b,
of the straight line is a simple index of the ex-vessel price
spread among the size categories of shrimp, i.e., it is an
index of ex-vessel price structure.

There were significant downward trends in b for brown
shrimp in all three coastal areas, and for white shrimp in
all coastal areas except the Texas coast from 1960 to 1978
(Table 4). For white shrimp from the Texas coast, the
general trend was downward, but it was not statistically
significant. The downward trends indicated that the May–
August ex-vessel price spread among the size categories
of shrimp increased from 1960 to 1978. Whitaker (1973)
also observed an increase in price spread between large and
small "southern" shrimp during the period from 1957 to
1971. The data point for 1972 was excluded from calcula-
tion of the trend for white shrimp from Pensacola to the
Mississippi River because no catch was reported for the
$\geq$ 68 count category in 1972 and, therefore, the fit of the
model was poor (Table 3).

May–August Cumulative Catch by Size Category

We calculated the cumulative weight, P, of the May–
August catch in each of the same seven size categories,
for each species, coastal area, and year (see Caillouet and
Koi 1980, 1981). These catches were cumulated, starting
with the size category of smallest shrimp (highest count,
$\geq$ 68) and continuing toward the size category of largest
shrimp (lowest count, 15–20). The following exponential
model described the relationship between P_i and C_i for each
species, coastal area, and year:

$$\hat{P}_i = c \, (\exp dC_i) \qquad (2)$$

where P_i = cumulative weight of the May–August catch in
the ith size category. The logarithmic form of model 2 was
used to estimate parameters c and d by linear regression
(Tables 5 through 7). The coefficients of determination
for the straight lines were very high. All slopes, d, were
negative, which reflected the construction of model 2 by
cumulating catches from small- to large-shrimp size categories
(see Caillouet and Koi 1980, 1981).

There were significant upward trends in d for brown
shrimp, but no significant trends in d for white shrimp, in
all three coastal areas from 1960 to 1978 (Table 4). The
upward trends indicated that the size of brown shrimp in
the reported May–August catches decreased from 1960 to
1978. The values of d for brown and white shrimp from
the Texas coast (Table 5) were lower than those from the
other two coastal areas (Tables 6 and 7), indicating that the
shrimp in the May–August catch from the Texas coast
generally were larger than those in the other two coastal
areas. The data point for 1972 was excluded from calcula-
tion of the trend for white shrimp from Pensacola to the
Mississippi River (Table 7) as in the previous section.

<div align="center">TABLE 4.</div>

Trends in ex-vessel value (dollars) per shrimp by size category, in cumulative catch (pounds, heads off) by size category, and in cumulative ex-vessel value (dollars) of catch by size category, for reported May–August catches (inshore and offshore combined) of brown and white shrimp from the Texas coast, the Mississippi River to Texas, and Pensacola to the Mississippi River during 1960–1978 (based on data from Tables 1–3, 5–7 and 9–11).

Species	Coastal Area		For ex-vessel value per shrimp by size category	For cumulative catch by size category	For cumulative ex-vessel value of catch by size category
Brown Shrimp	Texas Coast	Trends[1]	-0.0006^2	0.0024^2	0.0022^2
		Trend coefficients of determination	0.532	0.560	0.505
Brown Shrimp	Mississippi River to Texas	Trends	-0.0008^2	0.0003^2	0.0001
		Trend coefficients of determination	0.632	0.362	0.030
Brown Shrimp	Pensacola to Mississippi River	Trends	-0.0009^2	0.0010^2	0.0006
		Trend coefficients of determination	0.770	0.405	0.191
White Shrimp	Texas Coast	Trends	-0.0004	0.0003	-0.0001
		Trend coefficients of determination	0.179	0.006	0.000^3
White Shrimp	Mississippi River to Texas	Trends	-0.0007^2	0.0009	0.0003
		Trend coefficients of determination	0.378	0.160	0.017
White Shrimp	Pensacola to Mississippi River	Trends	-0.0007^2	-0.0006	-0.0015^4
		Trend coefficients of determination	0.365	0.086	0.294

[1] Represents slopes of the linear regressions of b, d, and h, respectively, on x, where x represents the last two digits of each year, 1960–1978. The values b, d, and h are defined in Tables 1–3, 5–7, and 9–11, respectively. Data for 1972 were excluded from regressions for white shrimp from Pensacola to the Mississippi River (see Tables 3, 7, and 11).

[2] The trend (slope) was significantly different from 0 at the 99% level of confidence.

[3] Indicates > 0.000 but ≤ 0.005, which would not round to 0.001.

[4] The trend (slope) was significantly different from 0 at the 95% level of confidence.

There were no significant correlations between the weight of the May–August catch (including "pieces," Figures 2 through 7) each year and corresponding levels of d (Table 8). A lack of correlation suggested that size composition was not the major factor affecting the weight of the May–August catch. This would be expected if another factor (e.g., year-to-year variations in recruitment) played a larger role than changes in size composition in determining variations in weight of the May–August catch.

May–August Cumulative Ex-vessel Value of Catch by Size Category

For each species, coastal area, and year, we calculated the cumulative ex-vessel value, D, of the catch in each of the seven size categories, starting with the size category of smallest shrimp and cumulating toward the size category of largest shrimp (see Caillouet and Koi 1980, 1981).

The following exponential model described the relationship between D_i and C_i for each species, coastal area, and year:

$$\hat{D}_i = g \, (\exp h C_i) \qquad (3)$$

where D_i = cumulative ex-vessel value of catch in the ith size category. The logarithmic form of model 3 was used to estimate parameters g and h by linear regression (Tables 9 through 11). Very good fits were indicated by the very high coefficients of determination. All slopes, h, were negative, reflecting the construction of model 3 by cumulating ex-vessel value of catch from small- to large-shrimp size categories.

Only the upward trend in h for brown shrimp from the Texas coast and the downward trend in h for white shrimp from Pensacola to the Mississippi River from 1960 to 1978 were statistically significant (Table 4). The upward trend for brown shrimp from the Texas coast indicated that the proportions of the ex-vessel value of the May–August catch represented by the size categories of smaller shrimp increased from 1960 to 1978. The downward trend for white shrimp from Pensacola to the Mississippi River indicated that the proportions of the ex-vessel value of the May–August catch represented by the size categories of larger shrimp increased from 1960 to 1978. The data point for 1972

TABLE 5.

Relationship between transformed cumulative weight (pounds, heads off) of catch, lnP, and count, C, for reported May–August catches (inshore and offshore combined) of brown and white shrimp from the Texas coast (statistical areas 18–21 combined), 1960–1978.*

Year	Brown Shrimp			White Shrimp		
	c	d	r^2	c	d	r^2
1960	183,811,255	−0.10258	0.934	7,182,658	−0.08253	0.783
1961	48,575,993	−0.07323	0.960	1,873,296	−0.03948	0.975
1962	23,996,295	−0.04965	0.922	2,666,134	−0.03786	0.951
1963	53,600,556	−0.06741	0.966	6,724,244	−0.07125	0.942
1964	42,618,117	−0.06161	0.971	5,706,520	−0.04442	0.991
1965	39,567,158	−0.04776	0.967	2,765,052	−0.03578	0.974
1966	36,003,258	−0.05231	0.963	3,536,330	−0.05257	0.959
1967	120,211,109	−0.06731	0.963	1,559,694	−0.03168	0.976
1968	88,261,098	−0.07819	0.926	3,392,237	−0.03486	0.896
1969	42,957,422	−0.05614	0.918	7,858,608	−0.06541	0.992
1970	44,769,157	−0.05286	0.968	8,412,422	−0.05276	0.976
1971	52,564,419	−0.05110	0.941	4,334,297	−0.08055	0.998
1972	87,278,961	−0.06344	0.948	7,807,770	−0.06981	0.966
1973	37,018,191	−0.03611	0.938	3,725,606	−0.03378	0.943
1974	47,553,217	−0.05093	0.964	8,407,460	−0.08301	0.972
1975	36,279,377	−0.03871	0.958	6,147,586	−0.07249	0.991
1976	33,851,030	−0.03720	0.971	3,487,480	−0.03433	0.991
1977	46,903,835	−0.03852	0.966	2,876,486	−0.02481	0.956
1978	29,219,592	−0.02498	0.934	4,231,047	−0.04206	0.946

*Based on the linear regression of lnP on C, where P = cumulative weight of May-August catch in each of seven size categories, C = lower limit (count) of each of the seven size categories, ln(c) = intercept, d = slope, and r^2 = coefficient of determination; all slopes, d, were significantly different from 0 at the 99% level of confidence, and the high r^2 values indicated a very good fit of the straight lines to the data points.

TABLE 6.

Relationship between transformed cumulative weight (pounds, heads off) of catch, lnP, and count, C, for reported May–August catches (inshore and offshore combined) of brown and white shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1960–1978.*

Year	Brown Shrimp			White Shrimp		
	c	d	r^2	c	d	r^2
1960	16,792,619	−0.01158	0.982	6,735,954	−0.03286	0.859
1961	9,683,268	−0.01507	0.980	746,104	−0.03511	0.935
1962	7,121,864	−0.00946	0.969	1,989,691	−0.04671	0.851
1963	19,298,733	−0.01274	0.970	22,225,926	−0.05003	0.847
1964	10,538,439	−0.01378	0.874	16,440,034	−0.06129	0.994
1965	16,842,736	−0.00975	0.997	7,148,335	−0.07295	0.986
1966	17,312,685	−0.00957	0.984	10,533,487	−0.05470	0.979
1967	31,665,870	−0.00988	0.979	7,354,846	−0.05329	0.995
1968	23,600,064	−0.00816	0.985	3,793,463	−0.02737	0.957
1969	20,210,847	−0.00425	0.998	7,408,659	−0.04606	0.959
1970	26,922,152	−0.00958	0.969	10,952,300	−0.03839	0.997
1971	30,789,368	−0.00887	0.970	13,765,830	−0.04732	0.995
1972	28,351,769	−0.01058	0.987	9,644,902	−0.05248	0.995
1973	16,561,644	−0.00387	0.996	3,607,660	−0.04251	0.992
1974	17,059,026	−0.00594	0.987	2,836,382	−0.02511	0.912
1975	13,688,820	−0.00535	0.989	4,586,097	−0.03938	0.955
1976	33,812,124	−0.00735	0.987	8,155,067	−0.02722	0.983
1977	48,701,481	−0.01097	0.972	7,897,209	0.02105	0.984
1978	45,423,493	−0.00804	0.946	9,211,470	−0.04247	0.995

*Based on the linear regression of lnP on C, where P = cumulative weight of May-August catch in each of seven size categories, C = lower limit (count) of each of the seven size categories, ln(c) = intercept, d = slope, and r^2 = coefficient of determination, all slopes, d, were significantly different from 0 at the 99% level of confidence, and the high r^2 values indicated a very good fit of the straight lines to the data points.

was excluded from calculation of the trend for white shrimp from Pensacola to the Mississippi River (Table 11) as in the two previous sections.

Simulations

Models 1 and 2 provided information useful in simulating the impacts of predictable changes in model parameters, barring any major changes in fishery management such as the closure of the FCZ off Texas. We conducted simulations to estimate what the overall average ex-vessel value per pound of the May–August catches of brown and white shrimp in the three coastal areas would have been for selected levels of b , to explore the possible consequences of changes in both the size composition of the catches and the ex-vessel price spread among size categories.

Because there were significant inverse relationships between ln(a) and b for both species in each coastal area (Table 8), we were able to estimate parameter a for selected levels of parameter b for each species and coastal area, to simulate V_i in equation 1. We then calculated the corresponding ex-vessel value per pound by size category

from the simulated V_i. In each case, we used the ex-vessel value per pound obtained for the 15–20 size category as an approximation of the minimum ex-vessel value per pound for the < 15 size category, because the model did not encompass the < 15 size category. We then multiplied the simulated ex-vessel value per pound in each size category by the reported pounds caught in each size category to simulate the ex-vessel value of the May–August catches by size category. The weight of catch in the category "pieces" was excluded from these calculations. The resulting values were summed over size categories to simulate the ex-vessel value of the May–August catches (pieces excluded). The simulated ex-vessel value was then divided by the reported May–August catch (pieces excluded) to obtain the simulated May–August average ex-vessel value per pound for each level of b for both species, for each coastal area, and for each year. Straight lines were fitted to the simulated ex-vessel value per pound versus d by linear regression (Table 12, Figures 8 through 13).

An increase in size of shrimp in the catches (as indicated by a decrease in d), coupled with an increase in price spread

TABLE 7.

Relationship between transformed cumulative weight (pounds,
heads off) of catch, lnP, and count, C, for reported May–
August catches (inshore and offshore combined) of
brown and white shrimp from Pensacola to the
Mississippi River (statistical areas 10–12
combined), 1960–1978.*

	Brown Shrimp			White Shrimp		
Year	c	d	r^2	c	d	r^2
1960	18,688,894	−0.03557	0.888	1,116,568	−0.01835	0.898
1961	9,525,281	−0.03397	0.932	141,706	−0.02710	0.911
1962	5,783,676	−0.02557	0.877	306,285	−0.03999	0.904
1963	20,786,826	−0.04541	0.895	1,028,879	−0.03534	0.944
1964	10,320,162	−0.02472	0.889	1,610,427	−0.03872	0.941
1965	18,107,921	−0.02888	0.816	575,779	−0.03509	0.923
1966	11,184,171	−0.01133	0.888	531,682	−0.02285	0.884
1967	22,420,583	−0.02483	0.870	816,760	0.02479	0.921
1968	20,390,303	−0.01797	0.884	499,633	−0.02806	0.923
1969	17,867,965	−0.02162	0.861	767,505	−0.03124	0.974
1970	17,263,241	−0.02010	0.890	1,360,986	−0.05002	0.977
1971	19,287,350	−0.01938	0.930	542,037	−0.06344	0.944
1972	14,473,790	−0.01703	0.938	21,844,069†	−0.22577†	0.937
1973	6,980,981	−0.01775	0.948	113,404	−0.04673	0.968
1974	8,348,897	−0.01229	0.929	155,550	−0.02484	0.871
1975	7,967,968	−0.01717	0.890	218,716	−0.03676	0.606
1976	12,660,152	−0.01700	0.882	331,522	−0.02700	0.918
1977	24,861,227	−0.02879	0.888	404,477	−0.02900	0.980
1978	13,224,609	−0.01398	0.874	616,522	−0.04736	0.988

*Based on the linear regression of lnP on C, where P = cumulative
weight of May-August catch in each of seven size categories, C =
lower limit (count) of each of the seven size categories, ln(c) =
intercept, d = slope, and r^2 = coefficient of determination; all
slopes, d, were significantly different from 0 at the 99% level of
confidence, and the high r^2 values indicated a very good fit of the
straight lines to the data points.

†Both c and d for white shrimp in 1972 are distorted because no
catch was reported for the ≥68 count category.

among size categories (as indicated by a decrease in b),
clearly results in pronounced increases in the average
ex-vessel value per pound for brown and white shrimp
(Table 12, Figures 8 through 13). Decreases in b produce
greater increases in ex-vessel value per pound than equiva-
lent decreases in d. Because catches also depend upon
recruitment each year (Christmas and Etzold 1977), the
simulated average ex-vessel value per pound can be used as
a multiplier for estimating the ex-vessel value for a given
weight of May–August catch of a given size composition,
for selected levels of b, for both species, and for each
coastal area.

DISCUSSION

The extent to which the exclusion of unreported catches
from our analyses affected our results and conclusions cannot
be determined. Because reported catches of shrimp are not
equivalent to actual catches, and because there are errors
in assignment of catches to size categories, size composition
of reported catches is not identical to that of actual catches.
Unknown portions of catches were not reported, e.g.,
shrimp discarded because they did not meet minimum size
limits or for economic reasons, catches by recreational
fishermen, catches sold directly to the consumer, and
catches by foreign fishing craft (prior to 1976). Also
unknown is the extent of errors of misclassification of
catches by size category as a result of shrimp-grading
practices. Such misclassification errors may average out in
aggregated catches. However, a thorough investigation of
the effects of shrimp grading practices ("machine grading"
and "box grading") on size distributions of shrimp assigned
to various size categories would be necessary to determine
the extent and magnitude of misclassification errors.

TABLE 8.

Linear regressions of catch (in millions of pounds, heads off; includes "pieces") on d, and ln(a) on b for reported May–August catches
(inshore and offshore combined) of brown and white shrimp from the Texas coast, the Mississippi River to Texas,
and Pensacola to the Mississippi River, 1960–1978 (based on data from Tables 1–3 and 5–7).

	Texas Coast		Mississippi River to Texas		Pensacola to Mississippi River	
	Brown Shrimp	White Shrimp	Brown Shrimp	White Shrimp	Brown Shrimp	White Shrimp[1]
For catch on d						
Slope	− 20.437	− 5.329	586.502	−16.268	48.870	0.874
Intercept	15.3468	1.8985	24.8956	3.6975	9.8000	0.4291
Coefficient of Determination	0.006	0.019	0.035	0.011	0.019	0.002
For ln(a) on b						
Slope	-103.513^2	-65.392^3	$- 95.262^2$	-78.860^2	-105.387^2	-70.076^2
Intercept	− 7.3187	− 5.1176	− 6.7862	− 5.7348	− 7.0505	− 5.2073
Coefficient of Determination	0.495	0.288	0.627	0.509	0.752	0.417

[1] Data for 1972 were excluded (see Tables 3, 4, 7, and 11).

[2] The slope was significantly different from 0 at the 99% level of confidence.

[3] The slope was significantly different from 0 at the 95% level of confidence.

TABLE 9.

Relationship between transformed cumulative ex-vessel value (dollars) of catch, lnD, and count, C, for reported May–August catches (inshore and offshore combined) of brown and white shrimp from the Texas coast (statistical areas 18–21 combined), 1960–1978.*

Year	Brown Shrimp			White Shrimp		
	g	h	r^2	g	h	r^2
1960	108,230,092	−0.11393	0.936	3,736,986	−0.09477	0.805
1961	36,397,112	−0.09024	0.963	1,311,025	−0.05347	0.974
1962	21,729,036	−0.06461	0.924	2,031,327	−0.05238	0.959
1963	45,022,368	−0.09025	0.970	4,415,890	−0.08604	0.955
1964	32,308,471	−0.07813	0.973	3,882,035	−0.06032	0.993
1965	32,423,045	−0.06730	0.964	1,852,691	−0.04951	0.969
1966	45,338,631	−0.07277	0.963	3,972,436	−0.06882	0.953
1967	110,407,652	−0.08742	0.967	1,105,745	−0.04500	0.963
1968	95,090,535	−0.09680	0.932	2,409,621	−0.04215	0.934
1969	52,890,802	−0.07507	0.918	12,070,439	−0.09252	0.989
1970	50,876,414	−0.07431	0.973	9,425,600	−0.07358	0.984
1971	79,798,080	−0.07275	0.947	7,645,440	−0.09942	0.998
1972	161,353,796	−0.08626	0.943	18,067,946	−0.09807	0.970
1973	79,172,534	−0.05277	0.929	7,133,410	−0.04512	0.944
1974	71,254,604	−0.07047	0.975	22,639,800	−0.11129	0.973
1975	88,198,455	−0.05577	0.961	20,209,432	−0.09447	0.992
1976	114,877,856	−0.06065	0.963	12,554,629	−0.05527	0.985
1977	131,374,161	−0.05818	0.969	5,995,621	−0.03921	0.986
1978	82,262,836	−0.04355	0.935	11,590,079	−0.05261	0.963

*Based on the linear regression of lnD on C, where D = cumulative ex-vessel value of May-August catch in each of seven size categories, C = lower limit (count) of each of the seven size categories, ln(g) = intercept, h = slope, and r^2 = coefficient of determination; all slopes, h, were significantly different from 0 at the 99% level of confidence, and the high r^2 values indicated a very good fit of the straight lines to the data points.

TABLE 10.

Relationship between transformed cumulative ex-vessel value (dollars) of catch, lnD, and count, C, for reported May–August catches (inshore and offshore combined) of brown and white shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), 1960–1978.*

Year	Brown Shrimp			White Shrimp		
	g	h	r^2	g	h	r^2
1960	6,294,080	−0.01689	0.984	2,791,110	−0.04070	0.912
1961	4,367,232	−0.02222	0.970	458,704	−0.04443	0.940
1962	3,779,680	−0.01413	0.978	1,465,285	−0.05469	0.890
1963	7,578,910	−0.02356	0.967	12,757,629	−0.06392	0.919
1964	4,030,859	−0.02011	0.932	11,132,619	−0.07464	0.996
1965	7,214,764	−0.01621	0.996	6,237,562	−0.08830	0.986
1966	9,857,173	−0.01814	0.989	10,406,072	0.06669	0.988
1967	13,749,184	−0.01786	0.984	7,436,940	−0.06960	0.993
1968	11,181,487	−0.01686	0.987	3,573,443	−0.04375	0.933
1969	9,291,959	−0.00974	0.990	8,477,109	−0.06181	0.980
1970	13,512,017	−0.01775	0.997	11,711,596	−0.05426	0.997
1971	19,940,033	−0.02048	0.980	22,632,331	−0.07031	0.996
1972	23,692,521	−0.02099	0.992	20,043,390	−0.07449	0.991
1973	16,002,252	−0.00780	0.992	7,756,874	−0.05436	0.992
1974	11,394,827	−0.01407	0.947	4,675,188	−0.04562	0.860
1975	13,595,100	−0.01574	0.971	13,742,173	−0.06326	0.963
1976	45,458,483	−0.01738	0.976	27,191,908	−0.04896	0.978
1977	70,647,268	−0.02095	0.990	16,625,530	−0.03588	0.992
1978	64,185,636	−0.01841	0.974	31,609,871	−0.06042	0.996

*Based on the linear regression of lnD on C, where D = cumulative ex-vessel value of May-August catch in each of seven size categories, C = lower limit (count) of each of the seven size categories, ln(g) = intercept, h = slope, and r^2 = coefficient of determination; all slopes, h, were significantly different from 0 at the 99% level of confidence, and the high r^2 values indicated a very good fit of the straight lines to the data points.

TABLE 11.

Relationship between transformed cumulative ex-vessel value (dollars) of catch, lnD, and count, C, for reported May–August catches (inshore and offshore combined) of brown and white shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), 1960–1978.*

Year	Brown Shrimp			White Shrimp			Year	Brown Shrimp			White Shrimp		
	g	h	r^2	g	h	r^2		g	h	r^2	g	h	r^2
1960	8,761,783	−0.04059	0.899	434,369	−0.02356	0.928	1970	10,598,256	−0.02754	0.936	1,304,382	−0.06316	0.985
1961	4,797,953	−0.03877	0.947	74,272	−0.03073	0.921	1971	16,749,182	−0.03108	0.953	964,900	−0.08604	0.945
1962	3,500,583	−0.02976	0.903	222,137	−0.04531	0.913	1972	14,545,322	−0.02534	0.964	44,865,514†	−0.24128†	0.962
1963	10,692,680	−0.05386	0.915	510,773	−0.04643	0.959	1973	10,432,119	−0.02715	0.960	280,896	−0.05838	0.976
1964	4,749,073	−0.03086	0.916	965,547	−0.04960	0.947	1974	7,185,100	−0.02093	0.972	209,025	−0.04113	0.773
1965	9,390,415	−0.03357	0.840	354,339	−0.04205	0.912	1975	12,592,349	−0.02780	0.923	565,050	−0.05625	0.664
1966	6,541,388	−0.01644	0.923	387,472	−0.02925	0.855	1976	22,694,655	−0.02691	0.913	952,133	−0.04408	0.888
1967	11,741,029	−0.03094	0.895	473,568	−0.03479	0.922	1977	47,094,652	−0.03979	0.925	1,127,846	−0.04917	0.979
1968	12,320,437	−0.02614	0.924	395,363	−0.03829	0.951	1978	22,804,307	−0.02376	0.913	2,196,268	−0.06417	0.985
1969	13,085,954	−0.03053	0.897	675,298	−0.03973	0.977							

*Based on the linear regression of lnD on C, where D = cumulative ex-vessel value of May-August catch in each of seven size categories, C = lower limit (count) of each of the seven size categories, ln(g) = intercept, h = slope, and r^2 = coefficient of determination; all slopes, h, were significantly different from 0 at the 99% level of confidence, and the high r^2 values indicated a very good fit of the straight lines to the data points.

†Both g and h for white shrimp in 1972 are distorted because no catch was reported for the ≥68 count category.

TABLE 12.

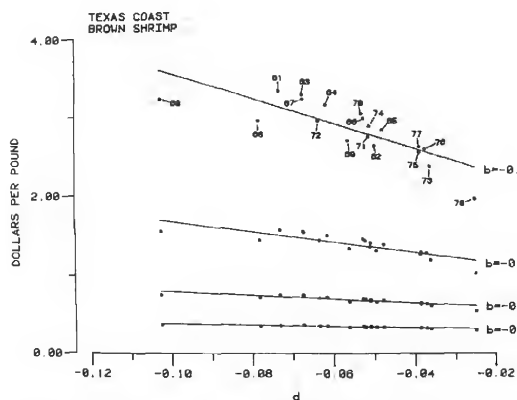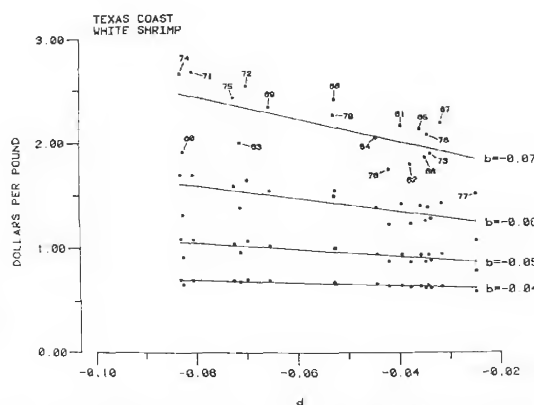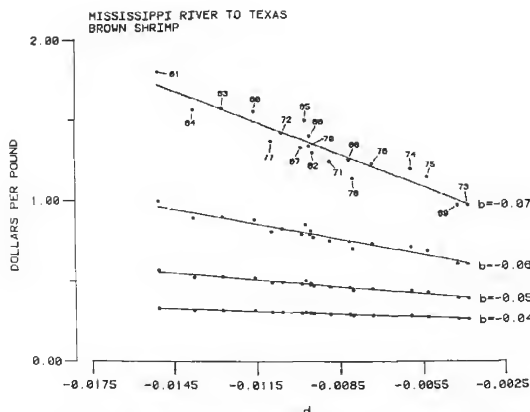Linear regressions of simulated average ex-vessel value (dollars) per pound (heads off) on d for reported May—August catches
(inshore and offshore combined) of brown and white shrimp from the Texas coast, the Mississippi River to Texas,
and Pensacola to the Mississippi River, 1960—1978, and for selected levels of b
(based on data from Tables 1—3 and 5—8).

| Species | Coastal Area | | b^1 | | | |
			−0.04	−0.05	−0.06	−0.07
Brown shrimp	Texas coast	Slopes	-0.8265^2	-2.4952^2	-6.4834^2	-15.7231^2
		Intercepts	0.2918	0.5404	1.0216	1.9686
		Coefficients of determination	0.761	0.724	0.694	0.666
Brown shrimp	Mississippi River to Texas	Slopes	-5.7716^2	-14.2613^2	-31.4732^2	-65.9078^2
		Intercepts	0.2432	0.3388	0.4837	0.7139
		Coefficients of determination	0.979	0.956	0.930	0.901
Brown shrimp	Pensacola to Mississippi River	Slopes	-3.1418^2	-8.4739^2	-20.4354^2	-46.6675^2
		Intercepts	0.3214	0.5283	0.8867	1.5235
		Coefficients of determination	0.959	0.956	0.950	0.942
White shrimp	Texas coast	Slopes	-1.4162^2	-3.2351^2	-6.1219^2	-10.6932^2
		Intercepts	0.5788	0.7834	1.0953	1.5770
		Coefficients of determination	0.745	0.598	0.501	0.433
White shrimp	Mississippi River to Texas	Slopes	-1.8251^2	-4.8334^2	-10.5496^2	-21.2666^2
		Intercepts	0.5165	0.7830	1.2303	1.9960
		Coefficients of determination	0.723	0.614	0.538	0.484
White shrimp	Pensacola to Mississippi River	Slopes	-3.0922^2	-8.5463^2	-18.2301^2	-35.2227^2
		Intercepts	0.5750	0.7221	0.9275	1.2195
		Coefficients of determination	0.726	0.557	0.475	0.424

[1] Levels of b selected for the simulations encompassed the observed ranges in b, for the most part.

[2] The slope was significantly different from 0 at the 99% level of confidence.

Figure 8. Simulated average ex-vessel value (dollars) per pound (heads off) for reported May—August catches (inshore and offshore combined) of brown shrimp from the Texas coast (statistical areas 18—21 combined), at selected levels of b over the range of d (based on data from Tables 1, 5, and 8). Lines fitted by linear regression (Table 12).
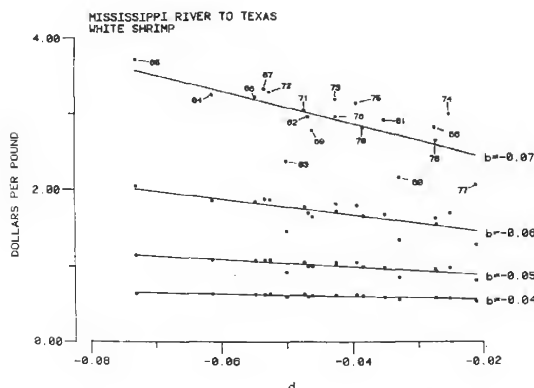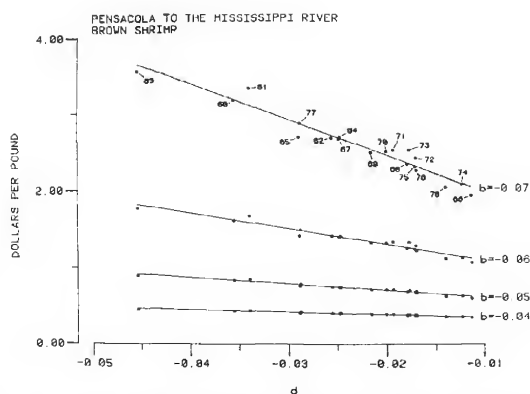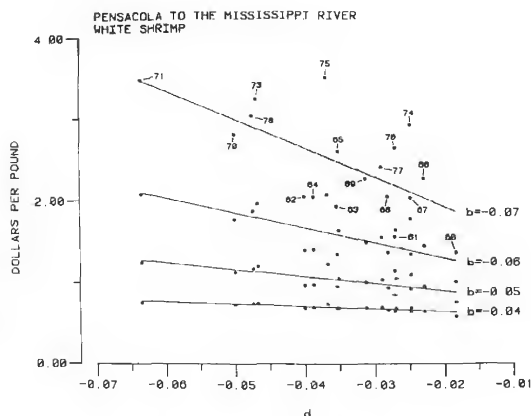

Figure 9. Simulated average ex-vessel value (dollars) per pound (heads off) for reported May—August catches (inshore and offshore combined) of white shrimp from the Texas coast (statistical areas 18—21 combined), at selected levels of b over the range of d (based on data from Tables 1, 5, and 8). Lines fitted by linear regression (Table 12).

Figure 10. Simulated average ex-vessel value (dollars) per pound (heads off) for reported May–August catches (inshore and offshore combined) of brown shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), at selected levels of b over the range of d (based on data from Tables 2, 6, and 8). Lines fitted by linear regression (Table 12).

Figure 12. Simulated average ex-vessel value (dollars) per pound (heads off) for reported May–August catches (inshore and offshore combined) of brown shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), at selected levels of b over the range of d (based on data from Tables 3, 7, and 8). Lines fitted by linear regression (Table 12).

Figure 11. Simulated average ex-vessel value (dollars) per pound (heads off) for reported May–August catches (inshore and offshore combined) of white shrimp from the Mississippi River to Texas (statistical areas 13–17 combined), at selected levels of b over the range of d (based on data from Tables 2, 6, and 8). Lines fitted by linear regression (Table 12).

Figure 13. Simulated average ex-vessel value (dollars) per pound (heads off) for reported May–August catches (inshore and offshore combined) of white shrimp from Pensacola to the Mississippi River (statistical areas 10–12 combined), at selected levels of b over the range of d (based on data from Tables 3, 7, and 8). Lines fitted by linear regression (Table 12).

There were significant decreases in size of brown shrimp in the reported May–August catches from the three coastal areas from 1960 to 1978. Caillouet et al. (1980) detected significant decreases in size of brown shrimp in reported annual catches from Texas and Louisiana from 1959 to 1976, and Caillouet and Koi (1980) detected significant decreases in size of brown shrimp in reported annual landings from the northern Gulf from 1961 to 1977. Fishing effort has increased substantially in the northern Gulf coast since 1960 (Christmas and Etzold 1977, GMFMC 1980).

For this reason, Caillouet et al. (1980) suggested that the observed decreases in size of brown shrimp may be the effects of increased fishing effort leading to the harvesting of increasing quantities of small shrimp before they grow to larger sizes. However, in the absence of a decline in total catch or conclusive evidence that shrimp are being harvested at rates in excess of that which would maximize yield, this cannot be construed as growth overfishing. The decrease in size of brown shrimp in catches from the Texas coast may be reversed as a result of closure of the FCZ off Texas due

to postponement of fishing until the shrimp grow to larger sizes. Coupled with continued increase in the price spread among size categories, an increase in size of brown shrimp in the Texas coast catch could greatly enhance the value of that catch. On the other hand, the closure may increase fishing effort along the coasts of Louisiana, Mississippi, and Alabama (GMFMC 1980), with the possible consequence of exacerbating the trends toward decrease of size of brown shrimp in the catches from these areas. In addition, the increased competition among offshore units could force some of the smaller ones to fish inshore as an alternative, thereby increasing the fishing pressure inshore.

To our surprise, there were no significant changes in size composition of reported May–August catches of white shrimp in the three coastal areas from 1960 to 1978. However, if fishing pressure on the white shrimp stock were increased as a result of closure of the FCZ off Texas, the size of white shrimp in the May–August catch could decrease. Caillouet et al. (1980), and Caillouet and Koi (1980) detected decreases in size of white shrimp in reported annual catches and landings, respectively, from the northern Gulf. Therefore, these decreases in size must have been generated by an overwhelming influence of size composition of the catches during months other than May–August.

Our analyses do not account for the impact of overall inflation on the trends in ex-vessel value of shrimp catches. However, they do indicate that the rate of inflation in ex-vessel value per shrimp is higher for larger than for smaller shrimp, a phenomenon that should be considered in studies of inflationary effects on the ex-vessel value of shrimp catches.

We have characterized the ex-vessel value per shrimp by size category, size composition, and ex-vessel value composition of the reported May–August catches of brown and white shrimp from the Texas, Louisiana, Mississippi, and Alabama coasts from 1960 to 1978. Comparisons, by similar analyses, with catch statistics for 1979, 1980, and 1981, should be of particular use and interest as one means of assessing the impacts of the closure of the FCZ off Texas.

ACKNOWLEDGMENTS

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January 1981

Trends in Ex-Vessel Value and Size Composition of Reported Annual Catches of Pink Shrimp from the Tortugas Fishery, 1960-1978

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TRENDS IN EX-VESSEL VALUE AND SIZE COMPOSITION OF REPORTED ANNUAL CATCHES OF PINK SHRIMP FROM THE TORTUGAS FISHERY, 1960–1978[1]

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ABSTRACT   Exponential models were used to characterize (1) ex-vessel value (in dollars) per shrimp by size category (count; i.e., number of shrimp per pound, heads off), (2) size composition (expressed as cumulative weight of the catch in pounds, heads off, by size category), and (3) ex-vessel value composition (expressed as cumulative ex-vessel value, in dollars, of the catch by size category) for reported annual catches (inshore and offshore combined) of pink shrimp (*Penaeus duorarum duorarum*) from the Tortugas fishery (statistical areas 1 and 2 combined) from 1960 to 1978. Exponents of the models were used as indices to investigate trends in ex-vessel value per shrimp, in size composition, and in ex-vessel value composition of the annual catches during that period. Both the spread in ex-vessel value per shrimp among size categories and the size of shrimp in the annual catches increased from 1960 to 1978. Also, the proportion of the ex-vessel value made up of shrimp of larger sizes increased from 1960 to 1978. This approach to analysis of catch statistics can be used to monitor the fishery, and the results can be compared with changes that may be brought about by permanently closing the Tortugas shrimp sanctuary in 1981, as proposed by the Gulf of Mexico Fishery Management Council in the fishery management plan for the shrimp fishery of the Gulf of Mexico.

INTRODUCTION

The fishery management plan for the shrimp fishery of the Gulf of Mexico, prepared by the Gulf of Mexico Fishery Management Council (GMFMC 1980), recommended permanently closing the Tortugas shrimp sanctuary (Figure 1) off southern Florida to all shrimping. The purpose of the closure is to protect small pink shrimp (*Peneaus duorarum duorarum*) so that they might survive and grow to sizes larger than 69 count (refers throughout this paper to number of shrimp per pound, with heads removed) before harvest. Essentially, this measure would reestablish most of the original Tortugas shrimp nursery which, until recently, had served as a sanctuary for pink shrimp recruited to the Tortugas and Sanibel shrimping grounds off southern and southwestern Florida, respectively. The management plan also encouraged the State of Florida to allow fishermen to retain all shrimp (including those of 69 count or smaller) caught in the open waters of the fishery conservation zone (FCZ), the area under federal jurisdiction beginning at the outer limit of Florida's territorial sea and extending 200 miles from shore.

Growth and mortality estimates by Lindner (1966) and Berry (1970) indicated that pink shrimp yield would be maximized if harvest were limited to shrimp larger than 70 count. However, Florida's minimum legal size limit of 70 count may have led to the discarding of large quantities of undersized pink shrimp caught in the FCZ. Thus, there is considerable interest on the part of the fishing industry, the State of Florida, the GMFMC, the National Marine Fisheries Service (NMFS), and fisheries scientists regarding

the potential impacts of permanently closing the Tortugas shrimp sanctuary on the yield of pink shrimp from the Tortugas fishery.

Apart from changes in yield caused by annual fluctuations in recruitment, changes in yield that may result from the closure probably will be accompanied by changes in size composition of the catch. Mean size is a simple criterion used for assessing status of an exploited stock (Henderson 1972, Ricker 1975). An increase in average size of individuals could indicate a decrease in mortality (usually equated with a decrease in fishing mortality) or an increase in growth. A decrease in average size might be brought about by retention of large quantities of small shrimp that formerly were discarded. Socioeconomic factors affecting strategies of fishing, culling of the catch, and marketing of the landings also could influence the size composition of the catch.

Caillouet et al. (1980) developed a simple exponential model to characterize the size composition (expressed as the cumulative percentage of weight of catch by size category) of reported annual catches of shrimp. Using a logarithmic transformation, they converted the model to one of a straight line, the slope (= exponent of the exponential model) of which was estimated by linear regression analysis. The model was used as an index to investigate fluctuations and trends in size composition of brown shrimp (*P. aztecus*) and white shrimp (*P. setiferus*) catches in Texas and Louisiana from 1959 to 1976. Caillouet and Koi (1980) modified the model by expressing size composition in terms of cumulative weight of catch by size category, instead of cumulative percentage of weight by size category. They used the modified model to investigate trends in size composition of the reported annual landings of brown, pink, and white shrimp from the Gulf and southeast coast fisheries of the United States from 1961 to 1977. They recognized
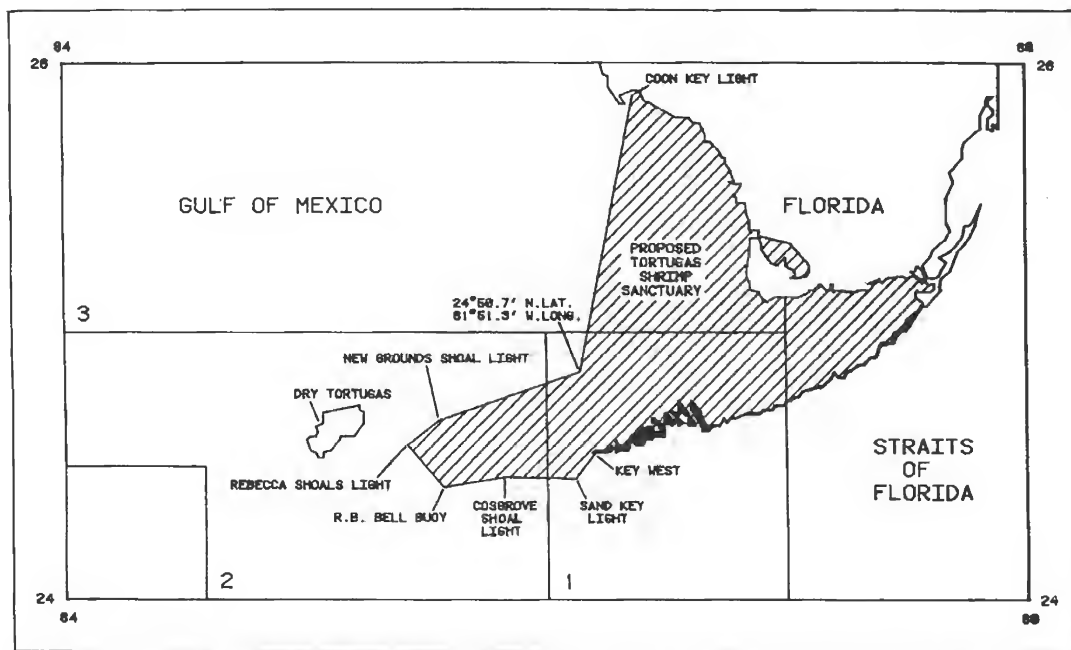
Figure 1. Boundaries of the Tortugas fishery (statistical areas 1 and 2 combined), the Tortugas shrimp sanctuary, the territorial sea, and the fishery conservation zone off south Florida (adapted from GMFMC 1980).

that the exponent of the model would be unaffected by the modification. They also used exponential models to investigate trends in the ex-vessel value per shrimp by size category and the ex-vessel value composition of the annual landings, and conducted simulations to predict the results of continued trends. Similar analyses were performed by Caillouet and Koi (1981) on reported May-August catches of brown and white shrimp from the Texas, Louisiana, Mississippi, and Alabama coasts from 1960 to 1978. The effect of shrimp size on the ex-vessel value of the catch has also been recognized by Neal (1967), Griffin et al. (1974), Griffin and Nichols (1976), and Griffin et al. (1976).

The NMFS has responsibility for monitoring the impacts of the permanent closure of the Tortugas shrimp sanctuary. The purposes of this paper are to propose a procedure for monitoring the Tortugas pink shrimp fishery based on the methods of Caillouet and Koi (1980), and to use their methods to investigate trends in ex-vessel value per shrimp by size category, size composition, and ex-vessel value composition of reported annual catches from 1960 to 1978. This approach then can be used as one means of assessing the impacts of permanently closing the Tortugas shrimp sanctuary and of retaining small shrimp harvested within the FCZ.

DESCRIPTION OF DATA

Annual summaries of the weight and ex-vessel value of the reported catches were compiled from data files available from the NMFS, Southeast Fisheries Center (SEFC), Technical and Information Management Services (TIMS), Miami, Florida. The weight of the reported annual catches (inshore and offshore combined) of pink shrimp from the Tortugas fishery (statistical areas 1 and 2 combined, Figure 1) was expressed in pounds (heads off), and the ex-vessel value in dollars, by size category (< 15, $15-20$, $21-25$, $26-30$, $31-40$, $41-50$, $51-67$, and ≥ 68 count, and "pieces") and by year (1960–1978). The "pieces" category represented parts of shrimp tails that could not be assigned to a numerical size category. Data for 1979 and 1980 were not available at the time of this writing.

English rather than metric units are used throughout this paper because they have been used historically, and information would be lost in their conversion to metric units. The reported annual catch represents that part of the actual annual catch reported by the NMFS, SEFC, TIMS, or its predecessor, the Bureau of Commercial Fisheries (BCF), U.S. Fish and Wildlife Service (USFWS).

ANALYSES AND RESULTS

Reported Annual Catches

Reported annual catches of pink shrimp from the Tortugas fishery showed a gradual downward trend from 1960 to 1978, while the reported ex-vessel value of these

catches showed an upward trend (Figure 2). However, the ex-vessel value was not adjusted to account for inflation.
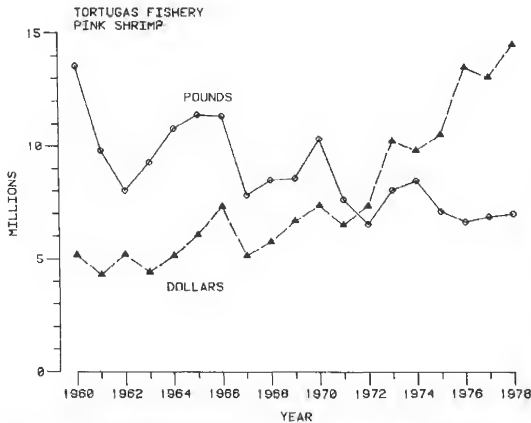

Figure 2. Weight (millions of pounds, heads off) and ex-vessel value (millions of dollars) of reported annual catches (inshore and offshore combined) of pink shrimp from the Tortugas fishery (statistical areas 1 and 2 combined), 1960–1978.

Annual Ex-vessel Value per Shrimp by Size Category

We divided dollars by pounds in each of seven size categories (15–20, 21–25, 26–30, 31–40, 41–50, 51–67, and ≥ 68 count) to obtain annual average ex-vessel value per pound by size category for each year. Next, we divided annual average ex-vessel value per pound in each of the seven size categories by the lower limit, C, of the respective size categories to obtain annual average ex-vessel value per shrimp, V, in each of the seven size categories for each year. Because lower limits of size categories were used as divisors, the calculated value per shrimp was the highest that could be obtained from the data for each size category.

The following exponential model described the relationship between V_i and C_i for each year:

$$\hat{V}_i = a\,(\exp bC_i) \qquad (1)$$

where V_i = annual average ex-vessel value per shimp for the ith size category, C_i = lower limit (count) of the ith size category (C_1 = 15, C_2 = 21, C_3 = 26, C_4 = 31, C_5 = 41, C_6 = 51, and C_7 = 68), and i = 1, 2, ..., 7. The logarithmic form of the exponential model was used to estimate parameters a and b by linear regression (Table 1). The high coefficients of determination, r^2, indicated that the fits of the straight lines to the points were very close. All slopes, b, were negative, reflecting the decrease in ex-vessel value per shrimp with increase in count (decrease in size). Note that the straight lines were obtained by a double transformation. The value per shrimp was transformed to natural logs, and the weight per shrimp (in pounds) was transformed to its reciprocal, count.

TABLE 1.

Relationship between transformed ex-vessel value (dollars) per shrimp, lnV, and count, C, for reported annual catches (inshore and offshore combined) of pink shrimp from the Tortugas fishery (statistical areas 1 and 2 combined), 1960–1978.*

Year	a	b	r^2
1960	0.08055	−0.05105	0.992
1961	0.07934	−0.04703	0.982
1962	0.10499	−0.04549	0.991
1963	0.11350	−0.05259	0.987
1964	0.10157	−0.05134	0.996
1965	0.09966	−0.04762	0.989
1966	0.10238	−0.04363	0.985
1967	0.12016	−0.04807	0.990
1968	0.14652	−0.05343	0.990
1969	0.16510	−0.05231	0.990
1970	0.16200	−0.05304	0.994
1971	0.22503	−0.06109	0.997
1972	0.31373	−0.06409	0.996
1973	0.25167	−0.05121	0.999
1974	0.28464	−0.05747	0.975
1975	0.31197	−0.05378	0.995
1976	0.51520	−0.05762	0.997
1977	0.44743	−0.05526	0.981
1978	0.40966	−0.05079	0.979

*Relationship was based on the linear regression of lnV on C, where V = annual average ex-vessel value per shrimp in each of seven size categories, C = lower limit (count) of each of the seven size categories, ln(a) = intercept, b = slope, and r^2 = coefficient of determination; all slopes, b, were significantly different from 0 at the 99% level of confidence, and the high r^2 values indicated very good fits of the lines to the data points.

Lower limits, rather than midpoints or upper limits of the seven size categories, were used in constructing model 1 because the size categories had unequal intervals, and an upper limit could not be determined for the ≥ 68 category. A lower limit of zero for the <15 size category was not realistic, and that category represented only a small fraction (≤ 1%) of the reported annual catches of pink shrimp from the Tortugas fishery. Therefore, the < 15 size category was excluded from model 1. Also excluded was the category "pieces," which represented parts of shrimp tails, assuming it represented the other size categories in proportion to their relative contributions to the catch. The constant, a, reflected the elevation of the straight line, which was influenced in part by our use of lower limits of size categories and exclusion of the < 15 size category in fitting the straight line. The slope, b, of the straight line is a simple index of the spread in ex-vessel value per shrimp among the seven size categories; i.e., the ex-vessel price structure.

There was a significant downward trend in b from 1960 to 1978 (Tables 1 and 2). This trend indicated that the differences in value per shrimp among the size categories increased with time; i.e., the value per shrimp increased more rapidly for larger shrimp than for smaller shrimp from

1960 to 1978. Whitaker (1973) also observed an increase in price spread between large and small "southern" shrimp during the period from 1957 to 1971.

	For ex-vessel value per shrimp by size category	For cumulative catch by size category	For cumulative ex-vessel value of catch by size category
Trends*	-0.0005†	-0.0009‡	-0.0012‡
Trend coefficients of determination	0.303	0.346	0.364

*Represent slopes of the linear regressions of b, d, and h, respectively, on x, where x is the last two digits of each year, 1960–1978.

†Indicates that the trend (slope) was significantly different from 0 at the 95% level of confidence.

‡Indicates that the trend (slope) was significantly different from 0 at the 99% level of confidence.

Annual Cumulative Catch by Size Category

We calculated the cumulative weight, P, of the catch in each of the same seven size categories for each year. Catch by size category was cumulated starting with the size category of smallest shrimp (highest count, ≥ 68), and continuing toward the size category of largest shrimp (lowest count, 15–20).

The following exponential model described the relationship between P_i and C_i for each year:

$$\hat{P}_i = c \, (\exp dC_i) \qquad (2)$$

where P_i = cumulative weight of catch in the ith size category. The logarithmic form of the exponential model was used to estimate parameters c and d by linear regression (Table 3). The coefficients of determination were high indicating close fits of the lines to the points. All slopes, d, were negative, which reflected the construction of model 2 by cumulating catch from small-shrimp to large-shrimp size categories. These slopes, d, would have been the same had they been calculated by the method of Caillouet et al. (1980).

The constant, c, reflected the elevation of the straight line and the magnitude of the annual catch, but c was influenced by our use of lower limits of size categories and exclusion of the < 15 size category in fitting the straight

line. The slope, d, of the straight line is a simple index of the size composition of the annual catch.

There was a significant downward trend in d from 1960 to 1978 (Tables 2 and 3). This indicated that the size of shrimp in the reported annual catches increased from 1960 to 1978.

Year	c	d	r^2
1960	28,961,850	-0.03542	0.947
1961	16,893,678	-0.02889	0.986
1962	19,594,706	-0.04238	0.952
1963	17,562,210	-0.02974	0.950
1964	21,648,787	-0.03264	0.941
1965	24,949,641	-0.03586	0.931
1966	26,482,905	-0.03863	0.924
1967	21,646,839	-0.04588	0.904
1968	26,254,291	-0.05073	0.904
1969	24,944,402	-0.04799	0.891
1970	23,114,946	-0.03684	0.898
1971	21,252,179	-0.04797	0.881
1972	22,106,008	-0.05647	0.852
1973	27,914,589	-0.05364	0.826
1974	27,500,370	-0.05349	0.881
1975	19,683,081	-0.04593	0.857
1976	18,398,874	-0.04559	0.848
1977	17,051,010	-0.04233	0.878
1978	15,703,277	-0.03979	0.924

*Relationship was based on the linear regression of lnP on C, where P = cumulative weight of annual catch in each of seven size categories, C = lower limit (count) of each of the seven size categories, ln(c) = intercept, d = slope, and r^2 = coefficient of determination; all slopes, d, were significantly different from 0 at the 99% level of confidence, and the high r^2 values indicated very good fits of the lines to the data points.

Annual Cumulative Ex-vessel Value of Catch by Size Category

We calculated the cumulative ex-vessel value, D, of the catch in each of the same seven size categories for each year. Ex-vessel value of catch was cumulated starting with the size category of smallest shrimp and continuing toward the size category of largest shrimp.

The following exponential model described the relationship between D_i and C_i for each year:

$$\hat{D}_i = g \, (\exp hC_i) \qquad (3)$$

where D_i = cumulative ex-vessel value of catch in the ith size category. The logarithmic form of the exponential model was used to estimate parameters g and h by linear regression (Table 4). Close fits of the lines to the points

were indicated by the high coefficients of determination. All slopes, h, were negative, which reflected the construction of model 3 by cumulating ex-vessel value of catch from small-shrimp to large-shrimp size categories.

TABLE 4.

Relationship between transformed cumulative ex-vessel value (dollars) of catch, lnD, and count, C, for reported annual catches (inshore and offshore combined) of pink shrimp from the Tortugas fishery (statistical areas 1 and 2 combined), 1960–1978.*

Year	g	h	r^2
1960	14,791,896	−0.04965	0.953
1961	9,023,023	−0.04032	0.988
1962	16,035,571	−0.05418	0.956
1963	11,014,906	−0.04335	0.958
1964	14,248,184	−0.04797	0.942
1965	16,841,893	−0.04747	0.938
1966	20,560,247	−0.04783	0.934
1967	18,349,264	−0.05825	0.919
1968	24,312,471	−0.06668	0.927
1969	26,218,347	−0.06296	0.916
1970	21,866,361	−0.05150	0.924
1971	28,397,169	−0.07106	0.899
1972	41,023,269	−0.08218	0.872
1973	49,716,628	−0.06940	0.850
1974	42,427,615	−0.07076	0.934
1975	43,790,173	−0.06451	0.858
1976	53,794,404	−0.06424	0.886
1977	41,799,294	−0.05768	0.925
1978	39,534,727	−0.05277	0.959

*Relationship was based on the linear regression of lnD on C, where D = cumulative ex-vessel value of catch in each of seven size categories, C = lower limit (count) of each of the seven size categories, ln(g) = intercept, h = slope, and r^2 = coefficient of determination; all slopes, h, were significantly different from 0 at the 99% level of confidence, and the high r^2 values indicated very good fits of the lines to the data points.

The constant, g, reflected the elevation of the straight line and the magnitude of the ex-vessel value of the annual catch, but g was influenced by our use of lower limits of size categories and exclusion of the < 15 size category in fitting the straight line. The slope, h, of the straight line is a simple index of the ex-vessel value composition of the annual catch.

There was a significant downward trend in h from 1960 to 1978 (Tables 2 and 4). This indicated that the proportions of the ex-vessel value of the catch represented by the size categories of larger shrimp increased from 1960 to 1978.

Size Composition and Annual Catch

There was no significant correlation (at the 95% level of confidence) between the weight of the annual catch (including "pieces," Figure 2), and the annual levels of d (Tables 3 and 5). A lack of correlation would be expected if another factor (e.g., recruitment) played a larger role

than variations in size composition in determining weight of the annual catch of shrimp.

TABLE 5.

Linear regressions of ln(a) on b, and of weight (in millions of pounds, heads off) of annual catch on d, for reported annual catches (inshore and offshore combined) of pink shrimp from the Tortugas fishery (statistical areas 1 and 2 combined), 1960–1978 (based on data from Tables 1 and 3).

	For ln(a) on b	For annual catch* on d
Slope	−77.035†	91.977
Intercept	−5.7697	12.5611
Coefficient of determination	0.428	0.170

*Expressed in millions of pounds (Figure 2). Includes "pieces."
†Indicates that the slope was significantly different from 0 at the 99% level of confidence.

Simulations

Models 1 and 2 provided information useful in simulating the impacts of further changes in ex-vessel price structure and size composition of the annual catches. Our simulations were based upon the hypothesis that the observed trends (Table 2) would continue, at least for a few years beyond 1978, were it not for the permanent closure of the Tortugas shrimp sanctuary. We conducted simulations to estimate what the average ex-vessel value per pound of past annual catches of pink shrimp would have been for selected levels of b, to explore the possible consequences of concurrent changes in size composition (as expressed by d) and ex-vessel price structure (as expressed by b).

Because there was a significant inverse relationship between ln(a) and b (Table 5), we were able to estimate parameter a for selected levels of parameter b, to simulate V_i in model 1. We then calculated the corresponding ex-vessel value per pound by size category from the simulated V_i. We used the simulated ex-vessel value per pound for the 15–20 size category as an approximation (minimum) of the ex-vessel value per pound for the < 15 size category. We then multiplied the simulated ex-vessel value per pound in each size category (including the < 15 size category) by the reported pounds caught in each size category to simulate the ex-vessel value of the catches in each size category for each selected level of b and for each year. Pounds caught in the size category "pieces" were excluded from these calculations. The resulting values were summed over size categories to simulate annual ex-vessel value of shrimp catches (pieces excluded) for each level of b and for each year. The simulated annual ex-vessel value was then divided by the reported annual catch (pieces excluded) to obtain simulated annual average ex-vessel value per pound for each level of b and for each year. Straight lines were fitted to

the simulated annual average ex-vessel value per pound for each level of b by linear regression (Table 6, Figure 3).

An increase in size of shrimp in the catch (as indicated by a decrease in d), coupled with an increase in price spread among size categories (as indicated by a decrease in b), resulted in a pronounced increase in the annual average ex-vessel value per pound for pink shrimp catches from the Tortugas fishery (Figure 3). Decreases in b produced greater increases in simulated annual average ex-vessel value per pound than did equivalent decreases in d.

TABLE 6.

Linear regressions of simulated average ex-vessel value (dollars) per pound (heads off) on d for reported annual catches (inshore and offshore combined) of pink shrimp from the Tortugas fishery (statistical areas 1 and 2 combined), 1960–1978, for selected levels of b (based on data from Tables 1, 3, and 5).

	b*			
	−0.04	−0.05	−0.06	−0.07
Slope	−1.3908†	−3.0989†	−6.0663†	−11.238†
Intercept	0.4609	0.6449	0.9219	1.3426
Coefficient of determination	0.854	0.788	0.715	0.648

*Levels of b selected for the simulations encompass as well as extend the observed range in b (see Table 1).

†Indicates that the slope was significantly different from 0 at the 99% level of confidence.

Figure 3. Simulated average ex-vessel value (dollars) per pound (heads off) for selected levels of b, the price structure index, over the range of d, the size composition index, for reported annual catches (inshore and offshore combined) of pink shrimp from the Tortugas fishery (statistical areas 1 and 2 combined), 1960–1978 (based on data from Tables 1, 3, and 5). Lines fitted by linear regression (see Table 6).

DISCUSSION

The extent to which the inclusion of unreported catches would have changed our results and conclusions cannot be determined. We assume that the bulk of the actual catches of pink shrimp from the Tortugas fishery was represented by the reported catches. Discarded undersized shrimp (GMFMC 1980) and shrimp landings sold to bait dealers probably constituted most of the unreported portion of the actual catches (T. J. Costello, NMFS, Miami, Florida, personal communication). A small part of the unreported portion of the actual catches also was made up of catches by foreign fishing craft prior to 1976, and of landings by recreational fishermen. Because the magnitude of the unreported portion of the actual catches was not known, size composition and ex-vessel value composition of the reported catches could be different from the size composition and ex-vessel value composition of the actual catches of pink shrimp from the Tortugas fishery. Furthermore, errors of misclassification of catches by size category occur as an outgrowth of differences in shrimp grading practices ("box" grading versus "machine" grading). However, the extent of such misclassification errors is unknown, as is their effect on size composition of the reported catches.

The trend of increase in ex-vessel price spread among size categories of shrimp, coupled with the trend of increase in size of shrimp in the catches, produced an even more pronounced trend of change in the ex-vessel value composition of the catches (Table 2). This helps explain why the ex-vessel value of the annual catches increased while the weight of the catches decreased from 1960 to 1978 (Figure 2). Inflation also accounted in part for the increase in ex-vessel value of the annual catches. While we did not determine the overall effects of inflation on the increase in ex-vessel value of the annual catches, our results clearly showed that this increase occurred partly because the rate of inflation in ex-vessel price was greater for large than for small shrimp. The results of our simulations (Figure 3) further illustrated the effects of concurrent changes in price spread and size composition.

Hooker (1972) and Toevs and Johnson (1978) suggested that the price of a given size category of shrimp depended on its relative abundance within the supplies available to the market. Hooker (1972) recognized that imported shrimp and cold storage holdings might influence size composition of available shrimp supplies, but postulated that the price spread was influenced more by the size composition of current landings. Size composition of the reported catches was determined by the combined effects of shrimp growth and mortality (natural and fishing), shrimp discarding, gear selectivity, shrimp grading practices, and catch sampling and reporting procedures. Finally, the price spread probably was influenced to some extent by the realtive demand for shrimp of various sizes.

In exploring possible causes of annual fluctuatons in size composition of catches (Table 3), we considered the

influences of major changes in regulations concerning the Tortugas fishery during the period from 1960 to 1978. For this purpose, we used an historical review of Florida legislation relating to management of the Tortugas fishery (Costello 1979). House Bill No. 2475, enacted in June 1961, redefined the geographical limits of the Tortugas shrimp beds, changed the size limits governing the opening and closing of the controlled area from 50 to 60 count, and established nursery areas within which no shrimping was allowed, except for live bait. Enactment of these regulations, intended to protect small shrimp, was followed by an increase in size of shrimp in the catch in 1962.

In 1963, the size composition was similar to that of 1961 (Table 3). In 1964, a trend of increasing size of shrimp in the catch began and continued through 1968. In 1969 and 1970, there again was a shift toward decreasing size of shrimp in the catch. We have no explanation for these changes.

Senate Bill No. 1370, enacted in July 1970, defined new boundaries for the Tortugas shrimp beds and prohibited shrimping, except for live bait, in those beds after July 1, 1970. It also repealed the size limit restriction governing the opening and closing of the controlled area, because the limit was no longer needed in the context of the redefinition of the Tortugas shrimp beds and the prohibition of shrimping in those beds. These regulations were intended to further restrict the catch of small shrimp. In 1971 and 1972, the size of shrimp in the catch increased (Table 3). Senate Bill No. 241, enacted in October 1972, made minor changes covering penalties for violations of regulations.

In 1973, the shrimping industry began to feel the effects of a critical fuel shortage. Increases in the cost of fuel may have encouraged shrimping closer to home ports. In 1973 and 1974, the size of shrimp in the catch decreased (Table 3). Senate Bill 505, enacted in April 1974, redescribed the boundaries of the Tortugas shrimp beds in unambiguous terms, as a response to previous court actions and to facilitate enforcement of regulations. However, there was limited enforcement of the seasonal closure of the controlled area to shrimping through 1978 (T. J. Costello, personal communication). In 1975, there was a substantial decrease in size of shrimp in the catch, and the trend of decreasing size continued through 1978. It remains to be determined what changes, if any, took place in 1979 and 1980, and what the impacts of permanently closing the Tortugas nursery area in 1981 may be on the weight, size composition, and ex-vessel value of the annual catch.

While the observed shifts in the size composition of the catch may have been related to historical changes in the regulations affecting the temporal-spatial distribution of fishing effort, it also could be argued that the changes in size composition may have been related to changes in quantity of fishing effort. Our analysis does not distinguish biological from socioeconomic influences on size composition of the catch, so any conclusions as to cause and effect are speculative at this time.

The trend of increase in ex-vessel price spread among

size categories of shrimp probably reflects trends in supply versus demand for shrimp of various sizes in the market. Differences in costs of harvesting shrimp close to ports versus farther from ports, as well as other factors, also may have affected the supplies of shrimp of various sizes and, therefore, the ex-vessel price spread. Further investigations of costs, supply and demand, inflationary effects, other economic factors, and changes in fishing effort are needed to explain the trends we observed (see Christmas and Etzold 1977, GMFMC 1980).

Future analyses similar to ours, based on additional catch statistics as they become available, will be one means of monitoring the Tortugas fishery. If the closure of the Tortugas shrimp sanctuary is effective in saving significant quantities of small pink shrimp to grow to larger sizes before harvest, an increase should occur in size of shrimp in the annual catch. On the other hand, if Florida allows shrimp ≥ 70 count caught in the FCZ to be retained rather than discarded by fishermen, and if the fishermen land and market significant quantities, that might decrease the size of shrimp in the annual catch.

As expected, our simulations show that the average ex-vessel value of a given weight of catch increases substantially when an increase in ex-vessel price spread among size categories is coupled with an increase in size of shrimp in the catch (Figure 3). This is reflected by the observed trend of increase in ex-vessel value of the annual catch despite the trend of decrease in weight of the catch (Figure 2), although the ex-vessel value of the catch also is influenced by inflation. However, at some point, further decrease in total weight of the annual catches may override the influences of increasing price spread among size categories and inflation. Thus, the ex-vessel value of the catch may reach an upper limit at some point when losses through natural mortality begin to override the increase in size of shrimp in the catch, the increase in the price spread between large and small shrimp, and the effects of inflation.

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January 1981

Observations of Deep-Reef Ichthyofauna from the Bahama and Cayman Islands, with Notes on Relative Abundance and Depth Distribution

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SHORT COMMUNICATIONS

OBSERVATIONS OF DEEP-REEF ICHTHYOFAUNA FROM THE BAHAMA AND CAYMAN ISLANDS, WITH NOTES ON RELATIVE ABUNDANCE AND DEPTH DISTRIBUTION

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ABSTRACT Observations of fish species inhabiting vertical wall habitats were conducted in the Bahama and Cayman islands. Twenty-three species from 12 families were recorded from various sites during the study. Number of species and abundance of individuals decreased with depth on the escarpments observed. *Gramma melacara* was the only species found throughout the depth ranges on all escarpments observed. Information about these habitats is sparse and more investigations are warranted.

INTRODUCTION

In situ observations of deep-reef fishes have been sparse, most often conducted from submersibles, as in Colin (1974, 1976) and Starck and Colin (1978). Observations of fish species inhabiting vertical wall habitats were conducted at three sites along the northernmost section of the Tongue of the Ocean in the Bahama Islands from September 22, 1980, through October 2, 1980, and on one site in the Cayman Islands, British West Indies, from November 21, 1980, through November 28, 1980 (Table 1).

TABLE 1.

Location, date, and depth of each wall dive conducted.

Site	Location	Geographical Location	Date	Depth of Dive
1	Chub Cay, Berry Islands	$25°22.5'$N $77°48.0'$W	9–25–80	61 m
2	Andros Island	$24°42.0'$N $77°43.5'$W	9–28–80	67 m
3	New Providence Island	$25°02.5'$N $77°34.0'$W	9–29–80	52 m
4	Little Cayman Island	$19°41.0'$N $80°03.5'$W	11–23–80	46 m

METHODS AND MATERIALS

All observations were conducted using SCUBA. Dives in the Bahama Islands were conducted from the R/V OLI of the Ocean Learning Institute in West Palm Beach, Florida. Dives off Little Cayman Island were conducted from the

beach. A total of 2.55 man-hours of underwater observation were completed. Fish counts were conducted by swimming over the escarpment edge to maximum depth and making observations upon ascent. Notes on the depth distribution and relative abundance of fish species encountered were written on a piece of plastic slate using a standard graphite pencil. Immediately upon surfacing from a dive, identification of fish species observed was compared with references from Bohlke and Chaplin (1968) and Randall (1968); underwater notes were transferred to a field notebook. Collection of specimens was not attempted due to the limited time available for each dive.

DESCRIPTION OF STUDY SITES

An abundance of hard corals, gorgonian corals, and sponges covered the wall habitats observed in this study, providing considerable habitat space for small cryptic fishes. Unfortunately, the limitations of using SCUBA at the depths encountered precluded anything more than a cursory examination of the species composition of the wall habitats.

The first observation site was located off the southern coast of Chub Cay, Berry Islands, in the Bahamas, approximately 2 miles offshore of Chub Cay Club Marina. The wall drop-off occurred at 37 m. The slope preceding the drop-off was marked by a series of ridges and channels, probably formed by sediment scouring. Coral growth was sparse on the slope, typically covering only the ridges. On the wall face, gorgonian corals and sponges were abundant with sparse hard coral growth. Small overhangs and crevices were abundant.

Site 2 was located off the eastern coast of Andros Island, Bahamas, about 2 miles offshore of Fresh Creek. The escarpment occurred at 46 m. Bottom topography and coral growth were similar to those described for Site 1.

Site 3 was located at the northwestern tip of New Providence, Bahamas. The escarpment was encountered at 15 m. Hermatypic coral growth above the escarpment was well developed. On the wall face, large formations were replaced by small coral heads, luxuriant gorgonian corals, and sponges. At approximately 24 m, a small horizontal ledge jutted out from the wall face. Below the ledge the wall was nearly vertical.

Site 4 was located off the northern coast of Little Cayman Island, British West Indies, about 1 mile offshore from Jackson's Point. The escarpment began at 21 m. Extensive reef development occurred on the shelf above the escarpment. A large ridge of staghorn coral occurred on the edge of the drop-off. The first 11 m formed a steep slope (approximately 50°), becoming nearly vertical at approximately 30 m. Again the wall face was occupied by an abundance of gorgonian corals, sponges, and small, low-profile heads.

RESULTS

Table 2 lists fish species observed, maximum depth of occurrence during observations, abundance estimates, and locality.

DISCUSSION

Thirteen of the 23 species recorded during this study also were reported from deep-reef escarpments in Jamaica and British Honduras by Colin (1974). As reported by Colin (1974), and by Starck and Colin (1978), *Gramma melacara* was by far the most abundant species on the deep wall faces observed during this study. Colin (1976) found *G. melacara* to be the most abundant fish from 90 to 110 m off Whale Cay, Berry Islands, Bahama Islands.

During observations off Chub Cay and Andros Island, both in the Bahamas, the escarpment was encountered in relatively deep water, 37 m and 46 m, respectively. Fish

TABLE 2.

Maximum depth of observation and abundance estimates of fish species observed during study.

Family, Genus, and Species	Site 1	Site 2	Site 3	Site 4	Species Abundance
			Observation Depths (m)		
Holocentridae					
Holocentrus rufus (Walbaum)			48		1 juvenile
Serranidae					
Cephalopholis fulva (Linnaeus)			24		2 adults
Epinephelus guttatus (Linnaeus)			24		1 adult
Hypoplectrus puella (Cuvier)		52			1 adult
Liopropoma sp.			50		1 adult
Mycteroperca bonaci (Poey)				30	1 adult
Serranus baldwini (Evermann and Marsh)		55			1 adult
Grammidae					
Gramma loreto Poey			24		Many adults and juveniles
Gramma melacara Bohlke and Randall	61	67	52	46	Very many adults and juveniles
Lutjanidae					
Lutjanus apodus (Walbaum)				28	4 adults
Ocyurus chrysurus (Bloch)				30	5 adults
Haemulidae					
Haemulon plumieri (Lacepède)		50			1 adult
Chaetodontidae					
Holacanthus tricolor (Bloch)			24	30	1 adult and 1 juvenile
Prognathodes aculeatus (Poey)			24	30	3 adults
Pomacentridae					
Chromis cyaneus (Poey)			24	30	Many adults
Chromis insolatus (Cuvier)			24		Many adults and juveniles
Chromis multilineatus (Guichenot)			24		Many adults
Pomacentrus partitus Poey	50	52			7 adults
Labridae					
Bodianus pulchellus (Poey)		52			1 juvenile
Clepticus parrai (Bloch and Schneider)			52	30	Many adults
Sphyraenidae					
Sphyraena barracuda (Walbaum)				40	4 juveniles
Gobiidae					
Gobiosoma sp.				46	1 adult
Tetraodontidae					
Canthigaster rostrata (Bloch)			24		1 adult

fauna associated with the sparse coral growth at the escarpment edge was represented by scattered individuals of the families Serranidae, Chaetodontidae, Pomacentridae, Labridae, and Scaridae. On the wall face off Chub Cay from 37 to 61 m, only two species were recorded, and off Andros Island from 46 to 67 m, only six species were recorded, four of which were represented by only one individual.

In contrast to the first two observations, observations off New Providence, Bahamas, and Little Cayman Island, B.W.I., revealed the escarpment in 15 m and 21 m of water, respectively. Coral growth at the escarpment edge was well developed, and the associated fish fauna was extensive. Over 60% of the species listed in Table 2 were recorded only from the New Providence and Little Cayman escarpments. I attributed this difference in abundance of species and individuals to the fact that the escarpment edge at those two sites was located in relatively shallow water, thus placing the "drop-off" in closer proximity to the highly populated shallow reef habitat. As observation depth on the vertical face of those walls increased, species abundance decreased, as did abundance of individuals with the exception of *Gramma melacara*.

I believe a secondary factor influencing species and individual abundance at site 3 was the occurrence of the horizontal ledge on the wall face approximately 9 m below the escarpment edge. Observations around that ledge revealed 9 of the 13 species recorded on that escarpment. I believe that reef fish probably migrate freely from the well-developed reef above the escarpment to the ledge and back, since the two sites are separated by only 9 m. *Gramma loreto* was common above the escarpment and was the most abundant fish at the ledge. Above the ledge on the wall face and below the ledge, *G. melacara* replaced *G. loreto*.

Overlap of the two species was slight, corresponding with the findings of Starck and Colin (1978).

It is likely that the differences in ichthyofauna between the shallow coral reef and the deep vertical wall face are influenced by water depth as well as by substrate orientation. More extensive observations along with acquisition of quantitative data would be required to arrive at any acceptable conclusions.

In situ observations and sampling are important to study adequately the deep reef and escarpment habitats. Open circuit SCUBA as well as deep submersibles have been used in these areas, and both have assets and drawbacks. Perhaps both methods used in conjunction would prove effective. Lock-out diving from a submersible is another alternative. More intense examination of this unique and interesting habitat type is warranted, as little is known of the ichthyofaunal species composition, community structure, and potential existence of undescribed species occurring there.

ACKNOWLEDGMENTS

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Gulf Research Reports

January 1981

First Recorded Observance of the Dinoflagellate *Prorocentrum minimum* (Pavillard) Schiller 1933 in Mississippi Sound and Adjacent Waters

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FIRST RECORDED OBSERVANCE OF THE DINOFLAGELLATE *PROROCENTRUM MINIMUM* (PAVILLARD) SCHILLER 1933 IN MISSISSIPPI SOUND AND ADJACENT WATERS[1]

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ABSTRACT   The present paper documents the occurrence of the dinoflagellate *Prorocentrum minimum* in Mississippi Sound and adjacent coastal waters. Outbreaks of discolored water are attributed to blooms of *P. minimum* in February 1977 and in January and February 1981. Data are presented on the seasonality of the organism in St. Louis Bay. Observations on water appearance and a descriptive analysis of the cells are presented for the 1981 blooms.

INTRODUCTION

Major outbreaks of discolored water caused by phytoplankton blooms periodically occur in Mississippi coastal waters (Perry et al. 1979, Eleuterius et al. 1981). In addition, the occurrence of localized plankton blooms appears to be commonplace and is suggested as the cause of fish kills and jubilees along the Mississippi coast (Gunter and Lyles 1979).

OBSERVATIONS

The most recent outbreaks of discolored water occurred

in Mississippi Sound and adjacent coastal waters in January and February 1981. Areas of "reddish" water were observed in the Sound south of the Intracoastal Waterway between the mainland and the east end of Horn Island and in St. Martin Bayou, an inlet off the Back Bay of Biloxi (Figure 1). Samples of the discolored water were taken by personnel of the Gulf Coast Research Laboratory parasitology section and given to the authors for analysis. Examination of these samples revealed the presence of large numbers of the dinoflagellate *Prorocentrum minimum*. Though the samples were not quantitative, cell numbers were estimated to be in the millions per liter. Water at the St. Martin Bayou site was reported to be viscous and "orange-brown" in color. Numerous spot (*Leiostomus xanthurus*) were observed swimming erratically or floating belly-up. No fish kills were
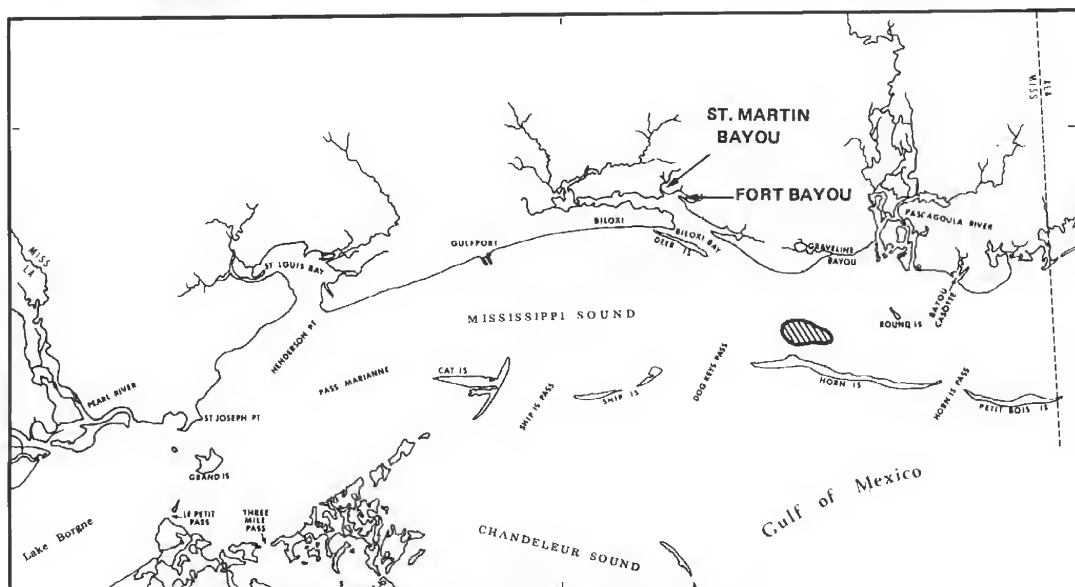
Figure 1. Bloom sites, Mississippi coastal waters.

reported in association with the bloom in the Sound. Hydrographic data were not available from either site.

From 1-ml sample aliquots placed on microscope slides, randomly selected cells were measured using an eyepiece micrometer (Table 1). Photomicrographs displaying cell characteristics are shown in Figure 2. Cells from the Sound site were slightly larger than those from the Bayou site. The anterior spine, characteristic of the genus, was present on most but not all of the specimens examined. The specimens exhibited subtle variations in shape from ovoid-quadrangular to near circular. Such variations in shape and presence or absence of the spine are typical of the species as seen in Hulburt's (1965) study of dense growths of *P. minimum* in New England estuaries. All specimens displayed poroid valve surfaces with striate margins (intercalary band), a large vacuole near the anterior end, and two flagella, one circular and one trailing, protruding from a shallow depression adjacent to the anterior spine. Although the majority of cells were free-swimming, clumps of up to 100 or more cells were frequently observed in the samples, possibly accounting for the "rust-colored" suspended sediment noticed at the Bayou site.

TABLE 1.

Measurements (N = 15) of *Prorocentrum minimum* cells collected in Mississippi waters. Standard error in parenthesis.

Site	Length (μ)	Width (μ)
Mississippi Sound	19.5 ($\pm$ 0.27)	19.3 ($\pm$ 0.32)
St. Martin Bayou	17.3 ($\pm$ 0.29)	17.3 ($\pm$ 0.34)

In addition to the 1981 blooms, the junior author observed a bloom of *P. minimum* in February 1977. Samples of discolored water were collected near the mouth of Fort Bayou (Figure 1) and brought to the Laboratory for analysis. All samples contained large numbers of *P. minimum*. The cells were estimated to be in the millions per liter, averaging between 18 and 20 microns in length and 14 to 16 microns in width. No hydrographic data were available.

Prorocentrum minimum appears to be an occasional component of the phytoplankton community in local waters. It was present periodically in phytoplankton samples collected from December 1977 through December 1978 at six stations in St. Louis Bay, Mississippi (Gulf Coast Research Laboratory, unpublished data). Peak abundance of 22,500 cells per liter occurred in March during a period of low salinity and high river discharge. The dinoflagellate was sporadic in occurrence from May through July, disappearing entirely from August through November. It reappeared in December 1978 and was more abundant at stations near the head of the Bay.

The St. Louis Bay observations are somewhat disparate
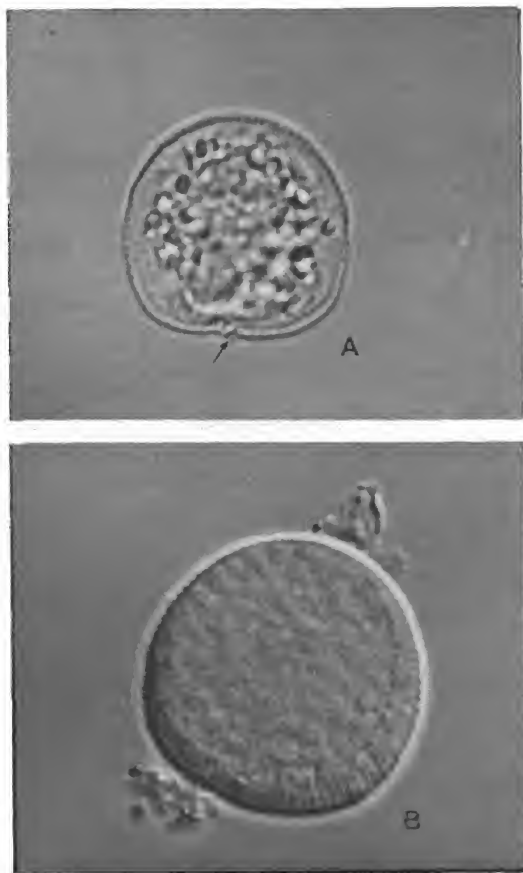
Figure 2. *Prorocentrum minimum*, Mississippi coastal waters. (A) Preserved specimen showing anterior spine (arrow). (B) Dried specimen showing poroid valve surface and striate margin (intercalary band). (Normarski optics, X 2300)

from those of Campbell (1973) who found *P. minimum* present throughout the year in the Gales Creek estuary of North Carolina, with densities reaching 206 cells per ml in April. Campbell described the species as euryhaline, occurring in salinities from 1 to 33 ppt (but seemingly preferring salinities toward the higher ranges), and eurythermal in temperatures from 3 to 31°C.

The authors regret that very little quantitative data have been collected that would suggest the factors contributing to the development of phytoplankton blooms in Mississippi coastal waters. Most observations are made in the course of routine sampling trips for various projects. To the present, there has been no baseline monitoring of biological, hydrological, and meteorological parameters that specifically may be of importance in producing and sustaining bloom conditions.

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January 1981

Preliminary Observations of the Effect of *Eimeria funduli* (Protozoa: Eimeriidae) on the Gulf Killifish *Fundulus grandis* and Its Potential Impact on the Killifish Bait Industry

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PRELIMINARY OBSERVATIONS OF THE EFFECT OF *EIMERIA FUNDULI* (PROTOZOA: EIMERIIDAE) ON THE GULF KILLIFISH *FUNDULUS GRANDIS* AND ITS POTENTIAL IMPACT ON THE KILLIFISH BAIT INDUSTRY[1]

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ABSTRACT   Liver infections of *Eimeria funduli*, a pathogenic coccidium, greatly affected growth of *Fundulus grandis* (Gulf killifish) maintained in an aquaculture facility for 55 days. At termination of the experiment, average weight gained by uninfected killifish was 877.5% compared to 308.0% in diseased fish. There appeared to be no correlation between mortality and disease in this study.

INTRODUCTION

Epizootics of *Eimeria funduli* Duszynski, Solangi, and Overstreet, 1979, a pathogenic hepatic coccidian of killifishes, have occurred in several coastal areas of the northern Gulf of Mexico and probably other areas (Solangi and Overstreet 1980, Fournie and Solangi 1980). Although 80 to 85% of both the liver and pancreatic tissues of heavily infected fish can be replaced by oocysts of *E. funduli* (Solangi and Overstreet 1980; Hawkins, Solangi, and Overstreet 1981), the disease does not appear to cause mortality in affected fish maintained in the laboratory. However, Solangi and Overstreet (1980) suspected that the parasite affected the growth of diseased fish.

The Gulf killifish *Fundulus grandis* is an important member of the salt marsh ecosystem, supports a growing bait industry, and can be reared commercially (McIlwain 1977; Solangi and Overstreet 1980; Tatum et al. 1978). Consequently, the disease could have a considerable impact on the economic potential of Gulf killifish.

This paper reports the effect of *E. funduli* on growth of *F. grandis*, possible impact of the coccidian on the killifish bait industry, and means of preventing the disease in aquaculture facilities.

MATERIALS AND METHODS

Laboratory-reared *Fundulus grandis* were obtained by stripping gravid male and female killifish collected from Halstead Bayou, Ocean Springs, Mississippi. Parasite-free fish were 2 1/2 months old at the beginning of the experiment, and were maintained in the laboratory at a temperature of $25 \pm 2°C$ and salinity of 20 ± 3 ppt. Infected individuals of the grass shimp *Palaemonetes pugio* Holthuis were collected from ponds adjacent to Halstead Bayou.

A group of 50 fish, randomly picked, were fed a single dose of infected grass shrimp to initiate the coccidian infections, whereas, 48 fish constituting a second group were fed Bama® Minnow Chow and they served as controls. Fish

in both groups were fed Bama® Minnow Chow throughout the remaining days of the experiment. Diseased and control fish were maintained in separate 3500-liter recirculating tanks containing 15 ppt seawater seeded with unicellular algae to provide supplemental food. Prior to being introduced into culture tanks, all killifish were weighed in grams and their total length measured in millimeters. At the end of the study, all surviving fish from both groups were weighed and measured. Growth was calculated by differences in weight gained and statistical analyses on the growth data were conducted using procedures of Campbell (1967) and of Steel and Torrie (1960).

RESULTS

Infections of *Eimeria funduli* had a considerable impact on growth of *Fundulus grandis* (Table 1). Infected killifish weighed significantly less than their uninfected counterparts. Diseased fish weighed an average of 24.8% more than uninfected fish prior to the experiment; however, by termination of the study (55 days) average weight of control fish exceeded that of parasitized fish by 91.6% (Table 1).

Eimeria funduli infections did not appear to cause mortality in this study. Survival of killifish after the 55-day experiment was 64.0% and 87.5% in control and diseased fish, respectively. However, most deaths occurred during the last 7 days of the study when there was an overnight decrease in water temperature from 26°C to 13°C.

DISCUSSION

In commerical bait-fish operations, about 45 to 52 days are required for killifish to reach marketable size (Tatum and Helton 1977; Tatum et al. 1978). Any factor that increases this grow-out period would reduce profits for bait-fish farmers. Based on data presented in Table 1, *E. funduli* greatly affects the growth of *F. grandis* maintained in an aquaculture facility and, consequently, could increase the grow-out period of killifish. Also, the assumed small stocks of *F. grandis* in panzootic areas reported by Solangi and Overstreet (1980) may be related to coccidian infections. Although, in view of our findings, it is apparent that the parasite could have a significant impact on the economic

TABLE 1.

Average weight (g) and total length (mm) gain of *Fundulus grandis* after 55-day infection of *Eimeria funduli*.

	Control				Diseased		
		Weight	Length[1]			Weight	Length[1]
	Number	Mean ± Standard Error	Mean ± Standard Error		Number	Mean ± Standard Error	Mean ± Standard Error
27 August 1980[2]	50	0.129 ± 0.008	18.66 ± 0.395		48	0.161 ± 0.001	19.58 ± 0.508
22 October 1980[3]	32	1.261 ± 0.261	43.41 ± 2.567		42	0.658 ± 0.023	38.67 ± 0.471
Average gain, %		877.5	132.6			308.0	97.5

[1] Average lengths of control and diseased fish at the beginning and termination of experiments are equal at 95% confidence limit (t-Test).
[2] Average weight of control fish is less than that of diseased fish at 95% confidence limit (t-Test).
[3] Average weight of control fish is greater than that of diseased fish at 95% confidence limit (t-Test).

potential of Gulf killifish, a detailed study on the effect of *E. funduli* on wild populations of killifish is urgently needed.

At present we do not have evidence suggesting a correlation between mortality and disease. Since most deaths in this study occurred during the period when the water temperature dropped abruptly, it appears that temperature shock coupled with undetermined stresses in the culture system could have contributed to the mortality. For the past 3 years we have maintained numerous groups of experimentally and naturally infected killifish in the laboratory for at least 3 months and have not witnessed any mortality. However, even though mortality cannot be ascribed to the parasite per se, heavily infected fish probably have difficulty surviving environmental and nutritional stresses.

To achieve maximum yield of killifish in bait operations, the parasite should be eliminated from the culture system. Although no chemotherapeutic treatment is available currently, isolation of the intermediate host from the culture facility appears to be the only practical alternative available

at this time. The grass shrimp and possibly other crustaceans serve as intermediate hosts (Solangi and Overstreet 1980), and have to be eaten to complete the life cycle. Exclusion of the infective intermediate host in pond-culture facilities, the predominant method of killifish rearing, can be a formidable task. On the other hand, closed recirculating systems such as the one developed by Ogle and Solangi at the Gulf Coast Research Laboratory in Mississippi appear to be an attractive alternative to pond rearing. In addition to effectively eliminating the intermediate host and providing good growth, the solar-heated recirculating system of Ogle and Solangi gives the aquaculturist control over many environmental factors not possible in pond culture.

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Gulf Research Reports

Volume 7 | Issue 1

Status of Turtles on the Mississippi Coast

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STATUS OF TURTLES ON THE MISSISSIPPI COAST

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ABSTRACT   Sea turtles have declined in numbers and federal agencies have become concerned with the numbers drowned in trawls by commercial shrimpers. Records are given of freshwater turtles and of the gopher tortoise in low-salinity waters. These include the Florida cooter *Pseudemys floridana*, the snapping turtle *Chelydra serpentina*, the alligator snapper *Macroclemys temmincki*, and the gopher *Gopherus polyphemus*. The diamondback terrapin *Malaclemys terrapin pileata* is common in brackish waters of Alabama and Mississippi. All sea turtles of the western Atlantic Ocean may be expected in Mississippi waters except for the Pacific ridley *Lepidochelys olivacea*, indigenous in northern South America in the Atlantic.

INTRODUCTION

In the past few years considerable interest in sea turtles has developed in the commercial shrimp fishery because of laws of the federal government. Turtles are caught in trawls of shrimp fishermen, and animals pulled for more than 2 hours or so are drowned. As a preliminary to some action, both State of Mississippi and United States authorities have asked the Gulf Coast Research Laboratory (GCRL) for a summary of information on sea turtles. These words are written as a summary of the information known about Mississippi coastal turtles.

CLASSIFICATION

The Order Testudinata of the Class Reptilia of the Sub-phylum Vertebrata includes all turtles that have lived on Earth. This group of animals arose during the Lower Triassic approximately 185 million years ago.

BRACKISH WATER TURTLES

A few freshwater turtles are washed down into low-salinity waters following freshets, floods, and rain storms on the coast. The writer once picked up a snapping turtle (*Chelydra serpentina*) at the mouth of Biloxi Bay (Gunter et al. 1973). Water salinity was 16.9 ppt.

During the period of August 26 through September 19, 1969, a unit of Seabees assisted in cleaning up the GCRL following Hurricane Camille of August 17–18, 1969. During that process, a very lively alligator snapping turtle (*Macroclemys temmincki*) was dug up from about 2 feet under the bottom of the innermost pond at the head of the boat slip. Salinity of the water was not taken. The pond was about 60 yards from the shore of Davis Bay, a tributary of Biloxi Bay. This turtle was dug up in September, virtually at the end of summer.

A gopher tortoise, *Gopherus polyphemus*, had a den between the buildings and the shore of Davis Bayou and every few days it swam the Laboratory boat slip and proceeded to high ground to the north. I never saw this event, but had it reported to me. I placed this turtle in a large sink of fresh water and found it floated very well. I made this

determination at the written instigation of Chapman Grant, who wondered if gopher tortoises could float.

Christmas and Waller (1973) reported three *Pseudemys floridana*, the Florida Cooter, from water with a salinity of 5.5 and 5.6 ppt from the lower Tchouticabouffa River.

The diamondback terrapin (*Malaclemys terrapin*) is the common turtle of low-salinity waters from Maryland to south Texas, and it has been divided into several subspecies along the way. In Mississippi, the subspecies *pileata* is common in low-salinity waters and in marshes, but seems to have fallen in numbers in recent years in the area of this Laboratory, possibly because of resurgence of the alligator. The same turtle is found in Alabama and, according to Mount (1975), it has declined in Mobile Bay due to Hurricane Camille in 1969.

All of the turtles listed above, except the diamondbacks and the gopher, are essentially freshwater species which only venture into low-salinity water as strays. The diamondback is essentially a brackish-water turtle; the gopher tortoise is terrestrial.

SEA TURTLES

Marine turtles have strong resemblances in that the feet are all flippers made for swimming and not much else. The largest is the leatherback turtle (*Dermochelys coriacea*) with parallel ridges down the back, and a leatherlike carapace undivided into plates. Ingle and Smith (1949) said a specimen from British Columbia weighed 1,450 pounds. It is worldwide in the tropics and subtropics, but not of great abundance anywhere. However, Leary (1957) reported seeing 100 along one rip current over a distance of 30 miles on the Texas coast. The leatherbacks belong to the Family Dermochelidae while all other sea turtles belong to the Family Cheloniidae. Although all species come close to shore and enter the estuaries at times, apparently all of them venture into the high seas and have been seen there far from land. However, they seem to be restrained by cold water. In North America, *Dermochelys coriacea* goes to Newfoundland and British Columbia. Its presence in most oceans led Hvass (1958) to say that it is probably the most widely distributed of all reptiles. De Sola (1939) said that the leatherback is the largest reptile on Earth, and he reported a weight of 1,900 pounds. However, I think that this is less

than the huge alligators this country formerly produced, one of which measured more than 19 feet in length.

Records of nesting of this species on the south Florida coast have been given by Caldwell et al. (1955), Allen and Neill (1957), and Caldwell (1959). Occurrence records and scattered nesting records of this turtle along the northern Gulf coast of Florida have been given by Yerger (1965).

We know of no other nesting records of this turtle elsewhere on the United States Gulf coast, but it is seen occasionally (see Leary 1957), and once I found a large dead one in Copano Bay, Texas, following a hard cold spell (Gunter and Hildebrand 1951).

Although we have no precise record of *D. coriacea* in Mississippi waters, we may assume with fidelity that, like the much rarer manatee, these animals occasionally swim through the waters of the state. Mount (1975) similarly has listed it in the salt waters of Alabama. Viosca (1961) in his listing of Louisiana turtles says of the leatherback, "Rare along our Coast."

The Atlantic loggerhead (*Caretta caretta*) is the largest chelonid. Caldwell et al. (1959) give the nesting range as from Cape Lookout, North Carolina, to the Caribbean Sea and Mexico. It has been tagged off South Carolina, and taken off Pass á la Loutre of the Mississippi River. The flesh is not highly esteemed and there is no known fishery for the species today. Groups of five or six of these turtles were seen off the western end of Horn Island in 1976, but we have no record on nesting in Mississippi.

The green turtle (*Chelonia mydas*) is noted for its culinary qualities and there are West Indian records of specimens up to 850 pounds. The animal is primarily herbivorus in contrast to the loggerhead. Several thousand acres of seagrasses in Mississippi Sound must be a special attraction to this species. Seagrass beds of Mississippi have been described by Eleuterius (1977).

According to Marquez-M (1966), the green turtle is called La Tortuga Blanca in Spanish because that is its color; the green refers only to internal fat, or calipash, which colors the soup. The eggs also have a greenish tinge. In some parts of the Pacific, the shells of cognate subspecies are almost black (Hirth 1971).

Until the turn of the century, the so-called green turtle and the ridley were shipped alive from south Texas ports to New York. These hapless animals were flipped onto their backs and carried that way on the open deck of coastwise steamers with the forelegs lashed together to impede struggles to right themselves. We might reasonably surmise that in heavy weather some of these were freed by being washed overboard, but it was not a common loss. The inability of sea turtles to right themselves was taken advantage of in their capture. One old Texas fisherman told me that the turtles came ashore on islands at night and went to sleep, whereupon fishermen crept up quietly and rushed about flipping the turtles on their backs; they returned and picked up the turtles later. In all likelihood the expression "turned turtle" derives from experiences of such a nature.

There seem to be no similar accounts of sea turtles on the Mississippi coast, but in 1918, over 337 pounds of green turtles were listed as sold (Rebel 1974, p. 116).

A record card in our turtle file is worded as follows:

Atlantic green turtle identified by David Burke, caught at Chandeleur, Louisiana, on 27 October 1972 by Mark Compton, a boatman. Turtle is about five or six years old and had 110 turtle barnacles, *Chelonibia testudinaria*, on his shell. He was caught in three feet of water. Carapace length 263 mm.

On August 21, 1972, Mr. Richard Waller saw a Gulf ridley at longitude 29°26'5"N and latitude 88°56'1"W. This is approximately 80 miles south of Horn Island, Mississippi.

Viosca (1961) said the ridley was the most abundant turtle off the Louisiana coast and that coincides with my observations over some 50 years off the northern Gulf coast. Viosca (1961) said the Gulf ridley preferred to nest in the loose sand of the Chandeleur Islands rather than the compacted beaches west of the delta of the Mississippi River. Apparently it formerly nested on the eastern coast of northern Mexico, and the adults extended to the Bermudas and occasionally to the British Isles. There is a cognate species on the western coast of Mexico and on the Pacific coast, generally.

The ridley is the smallest of the edible sea turtles. It has no known large nesting grounds on the northern Gulf coast. It is a small white turtle growing to about 100 pounds in size. Fishermen often take it home to eat when it is caught.

It has been noted in the case of the leatherback, the green turtle, and the Gulf ridley, that there is a peculiar gap in the distribution of young growing turtles. From the time the young escape to sea until the adults come ashore to lay, the intermediate sizes are not seen. Intermediate sizes are extremely rare and virtually unrecorded. Carr (1967) expounded on this matter at some length. This situation is not unknown in other animals and is particularly puzzling in the case of the tarpon. With regard to turtles, it may well be that the young ones hunt attached beds of sargassum or even the floating sargassum. Here the trouble is that the distribution of attached and floating sargassum is very diffuse and not well known. It could be that one little turtle per square mile would absorb all the annual production from La Tortuguero, the Costa Rican nesting area, without appearing excessively numerous.

The hawksbill (*Eretmochelys imbricata* Linnaeus) has such a glistening, beautiful shell compared to all other turtles that it must be seen to be believed. The flesh is not favored and, in the Far East, it is said to be poisonous at times (De Sola 1939). In the northern Gulf only animals 1½ feet in carapace length or less are seen. In the southern Caribbean specimens 3 feet in carapace length have been reported. Most biologists who spend time afloat have seen a few hawksbills in the northern Gulf. They are reputed

to be active and aggressive. Mr. Richard Waller of this Laboratory once took a foot-long specimen at the surface about 40 miles south of Horn Island, Mississippi, where it was apparently asleep on a floating mat of sargassum. His chief impression was of the terrible fright of the captured animal and its violent attempts to escape. Because of that he let it go in a very short while. The hawksbill is not known to nest on the northern Gulf coast.

SOME GENERALITIES AND MINOR POINTS

Turtles were contemporaries of early dinosaurs and they have long outlived them. Their evolutionary strategy has been highly successful even though there seems to be a temporary recession of sea turtle populations caused by over-exploitation by man. Carr (1967) has suggested that this crisis may be met by a successful cultivation of turtles. The recent increased interest in mariculture gives some hope for this development.

Wetjen (1948) and Carr (1967) have documented the great importance of sea turtles in the tropics of two and three generations ago. Carr (1967) has also told about the decline, but he has outlined a hopeful prognostication regarding management.

A laying place for the green turtle still exists in Costa Rica; one for the Gulf ridley on the northeastern Mexican coast recently died out (see Carr 1967). Nesting of the hawksbill probably has occurred only in the Caribbean region in historic times. There are reported single or scattered nestings of the ridley, leatherback, green turtle, and loggerhead on the Gulf and South Atlantic coasts north to Virginia from time to time, and apparently these scattered nestings now maintain the species. Hopefully they will continue to do so until mankind remarshals its conservation forces and comes to the rescue of these antediluvean monsters which have existed for about a fifth of a billion years.

Back in the first decades of this century, when diamond-back terrapins were selling for as high as $90 a dozen, S. F. Hildebrand (1929) was successful in raising these animals; commercial ventures also were successful in Louisiana, North Carolina, and Virginia. However, when wine was prohibited, preeminence of turtle soup declined, and sales of turtles and calipash declined as prices fell. Similarly, hawksbills were given some respite by the invention of a synthetic substitute for turtle shell.

Several authors state that marine turtles never come ashore except to lay their eggs and that only the females, of course, come ashore. However, Stebbins (1954) said that various Pacific species come ashore to "bask", and other authors said they come ashore to sun themselves. In this connection we should note from the statement above that turtles along the Texas coast come ashore at night to sleep.

The leatherback is said to be one of the fastest of all swimmers. It has been stated that they can get up to 32 miles per hour, but I have seen no precise clockings of the swimming speed of this animal. But we may conclude that it is a very fast swimmer when disturbed or startled because it has impressed various observers. In the literature there are also statements that this turtle likes to remain at depths of 150 feet, but I have seen no statements as to how this was determined. With the exception of the ridley, female turtles come ashore after dark at which time they may be scared back to the water by the distant striking of a match, according to Carr (1967). The ridleys, in contrast, will crowd ashore in the daytime, or at least the Gulf subspecies does so.

There is a peculiar anomaly in the distribution of the Pacific ridley. This species is also found in the southern Caribbean in the Guianas, but nowhere else on the eastern shores of the western hemisphere. Carr (1967) discussed this at length and showed that these animals were also found on the West African shore. He assumed that it comes around Africa from the east and is connected with Pacific ridleys all the way around the world to the western shore of Mexico. An alternate theory may be that this population was cut off from the Pacific when Isthmus America was formed approximately 5.7 million years ago (Emiliani et al. 1972). In any case the Gulf species of this turtle is found only in the Atlantic but the Pacific subspecies is found widely in the Pacific and also in the restricted area of Atlantic South America.

In summary, on the eastern shores of the western hemisphere we have *Dermochelys coriacea, Eretmochelys imbricata, Caretta caretta, Chelonia mydas, Lepidochelys kempi,* and *L. olivacea.* The Pacific species generally are given subspecific standing. Sea turtles were very numerous in Colonial days; they were widely used as food. In some cities such as Charleston, South Carolina, their eggs were highly prized for the baking of cakes. All species seem to have declined greatly in the past 100 years, but it is to be hoped that, as the knowledge of their biology increases, effective conservation measures will lead to restoration of their populations.

The most recent review is that of Rebel (1974). It cites most of the literature and gives information on past commercial production in the Gulf and South Atlantic areas.

Just as this manuscript was completed the volume containing the recent study of south Texas sea turtles by Rabalais and Rabalais (1980) was received. It must be mentioned in connection with the present remarks. The hawksbill (*Eretmochelys imbricata*) and the leatherback (*Dermochelys coriacea*) were listed as rare and strandings of these two were not listed, although sightings and previous records were given. Subadult loggerheads (*Caretta caretta*) were listed as the most abundant turtles on the south Texas coast with Kemp's ridleys as the second most abundant. Sporadic nesting of ridleys and green turtles on Padre Island was noted.

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January 1981

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OBSERVATIONS ON THE DISTRIBUTION AND SEASONALITY OF PORTUNID MEGALOPAE IN MISSISSIPPI COASTAL WATERS[1]

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ABSTRACT   Observations on the distribution and seasonality of common coastal portunid megalopae are presented. *Callinectes sapidus* megalopae were abundant from May through November. The megalopae of *C. similis*, though present throughout the year, peaked in numbers from February through April. With the exception of January, *Portunus* spp. megalopae occurred in all months, with maximum numbers collected in April. *Callinectes sapidus* megalopae commonly occurred at all stations, whereas, the megalopae of *C. similis* and *Portunus* spp. appeared to be limited by salinity.

INTRODUCTION

There have been few studies on the distribution of portunid larvae in coastal and offshore waters of the north central Gulf of Mexico. In Texas, Daugherty (1952), More (1969), and King (1971) discussed the movement of *Callinectes* megalopae through coastal passes. In Louisiana, Darnell (1959) speculated on the occurrence of blue crab larvae in Lake Pontchartrain, and Adkins (1972) presented data on the seasonality of blue crab larvae from Whiskey Pass. Andryszak (1979) studied the summer distribution of brachyuran larvae in offshore waters of southeastern Louisiana. The distribution of *Callinectes* larvae in Mississippi coastal waters was investigated by Perry (1975). Menzel (1964) studied the summer distribution of blue crab larvae in Gulf waters off Alligator Harbor, Florida. The present study is the first in which the distribution and seasonality of *C. sapidus* Rathbun, 1896, *C. similis* Williams, 1966, and *Portunus* spp. megalopae are treated separately.

MATERIALS AND METHODS

Monthly quantitative nekton samples were collected in Mississippi coastal waters from July 1974 to September 1979, using 1-m nekton nets fitted with 1,050-μ netting. Nets were equipped with flowmeters, and opening and closing devices. Simultaneous, 20-minute surface and bottom tows were taken at sites 3 miles south of (1) Horn Island Pass (station 86), (2) Dog Keys Pass (station 84), and (3) Ship Island Pass (station 82). All portunid megalopae were removed from the samples, counted and identified. In samples containing over 200 megalopae, an aliquot of 100 specimens was examined. Identifications were made using characters developed in a concurrent rearing program in which megalopae were collected monthly for 1 year and reared through early crab stages in the laboratory.

RESULTS AND DISCUSSION

A total of 33,422 portunid megalopae was recovered from the 360 nekton samples examined (Table 1). The megalopae of *Callinectes sapidus* composed 70.8% of the total catch; *C. similis*, 11.5%; *Portunus* spp., 17.5%; and other Portunidae, < 0.1%. Although several species may be included under *Portunus* spp., all reared *Portunus* megalopae were *P. gibbesii*. Included under "other Portunidae" were several specimens of an undescribed giant megalopa and another undescribed form which appeared to share characters distinctive of both *Callinectes* and *Portunus*.

TABLE 1.

Total catch of portunid megalopae by taxa.

Taxa	Total Catch*	Total Standard Catch†	% of Standard Catch
Callinectes sapidus	24,171	31,681.1	70.8
C. similis	4,396	5,157.3	11.5
Portunus spp.	4,839	7,853.0	17.6
Other Portunidae	16	21.0	< 0.1
Total	33,422	44,712.4	100.0

*The sum of megalopae caught (number/20-minute tow) from each sample.

†The sum of the standardized numbers (number/1,000 m^3) of megalopae from each sample.

Concurrent trawl data were taken in coastal and estuarine waters. *Callinectes sapidus* juveniles and adults constituted approximately 53% of the total catch while *C. similis* contributed 38%; *Portunus* spp., 9%; and other portunids, < 1.0%.

Total catch of portunid megalopae at all three stations was similar; however, the percent composition of the catch differed greatly (Table 2).

TABLE 2.

Catch of major portunid taxa by station.

Station	Taxa	Total Catch*	Total Standard Catch†	% of Standard Catch
86	C. sapidus	6,662	7,950.2	49.5
	C. similis	2,730	3,159.7	19.7
	Portunus spp.	2,882	4,932.6	30.8
	Total	12,274	16,042.5	100.0
84	C. sapidus	7,672	11,851.9	73.1
	C. similis	1,431	1,739.9	10.7
	Portunus spp.	1,709	2,624.9	16.2
	Total	10,812	16,216.7	100.0
82	C. sapidus	9,837	11,880.9	95.5
	C. similis	235	257.7	2.1
	Portunus spp.	248	295.5	2.4
	Total	10,320	12,434.1	100.0

*The sum of megalopae caught (number/20-minute tow) from each sample.

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Station 86 contributed 35.9% of the total catch consisting of *C. sapidus* (49.5%), *C. similis* (19.7%), *Portunus* spp. (30.8%), and unidentified Portunidae (0.1%). Station 84 yielded 36.3% of the total catch consisting of *C. sapidus* (73.1%), *C. similis* (10.7%), and *Portunus* spp. (16.2%). Station 82 was somewhat less productive, providing 27.6% of the total catch. *Callinectes sapidus* dominated the catch (95.5%), with *C. similis* (2.1%) and *Portunus* spp. (2.4%) far less abundant.

Overall percent composition as well as total numbers of *C. sapidus* megalopae increased from east to west, whereas the catch of *C. similis* and *Portunus* spp. was greatly decreased. This trend corresponds with an east-west salinity gradient characteristic of Mississippi coastal waters. Salinities were highest at station 86 throughout the sampling period with bottom waters averaging 32.1 ppt and surface waters, 25.5 ppt. A similar salinity regime was noted at station 84; bottom waters averaged 31.4 ppt and surface waters averaged 25.1 ppt. Salinities were lowest at station 82, averaging 28.3 ppt for bottom and 23.5 ppt for surface waters, with individual values seldom above 30.0 ppt. Although information on salinity preference of *C. similis* and *Portunus gibbesii* megalopae is not available, adults and juveniles are known to prefer coastal waters of high salinity (Christmas and Langley 1973). Bookhout and Costlow (1974) reported that salinities below 30.0 ppt were not favorable for development of *Portunus spinicarpus* larvae. Salinities optimal to maximum survival of *C. sapidus* megalopae (Costlow 1967) were observed at all stations, however; *C. sapidus* megalopae were more abundant at the lower salinity station 82. King

(1971) reported greatest influx of *Callinectes* sp. megalopae to occur at 26.0 ppt salinity in Cedar Bayou.

Based on overall catch, portunid megalopae showed no affinity for surface or bottom waters (Table 3). Although twice the number of *C. similis* megalopae were caught in surface than bottom waters, the difference can be accounted for by a single large catch (1,434.8/1,000 m^3) taken at station 86 in March 1976. Most (15 of 20) large catches of *C. sapidus* megalopae (300+/tow) were taken on rising or peak tides; however, no preference for surface or bottom waters was observed. Individual large catches (100+ individuals) of *C. similis* and *Portunus* spp. megalopae were commonly taken during both rising and falling tides.

TABLE 3.

Catch of major portunid taxa by depth.

	Taxa	Total Catch*	Total Standard Catch†	% of Standard Catch
Surface	C. sapidus	11,534	13,632.6	65.2
	C. similis	3,290	3,780.3	18.1
	Portunus spp.	2,467	3,493.5	16.7
	Total	17,291	20,906.4	100.0
Bottom	C. sapidus	12,637	18,048.4	75.9
	C. similis	1,106	1,377.1	5.8
	Portunus spp.	2,372	4,359.5	18.3
	Total	16,115	23,785.0	100.0

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Previous reports on the vertical distribution of *Callinectes* megalopae appear conflicting. Williams (1971), King (1971), Perry (1975), and Smyth (1980) reported *Callinectes* megalopae to be in greatest abundance in surface waters. In contrast, 96% of the *Callinectes* megalopae collected by Tagatz (1968) and all of the megalopae collected by Sandifer (1973) were from bottom waters.

A definite seasonal pattern of abundance for portunid megalopae was observed (Figure 1). *Callinectes similis* megalopae were collected throughout the year, occurring in greatest abundance from February through April with a March peak. This was followed by an April peak of *Portunus* spp. during which concentrations of up to 1,670.3/1,000 m^3 were observed. *Callinectes sapidus* megalopae were collected in every month except January and February. Two peaks in abundance were observed, the first in late spring-early summer, and a second, larger peak in the late summer-early fall during which maximum densitites of 2,530.8/1,000 m^3 were obtained. Large catches of *C. sapidus* megalopae were not made between December and April.
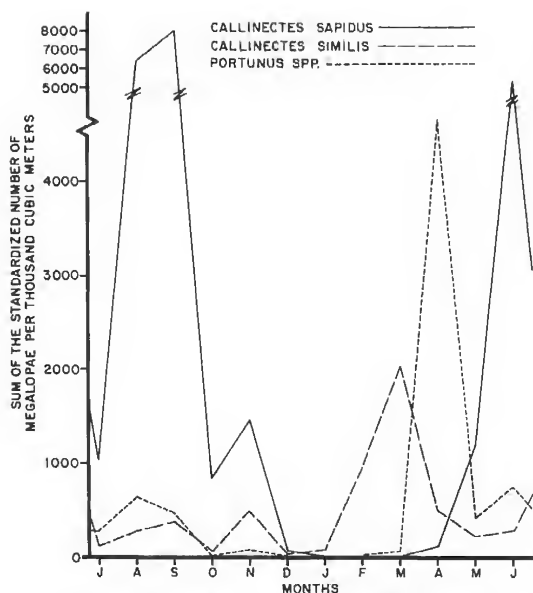
Figure 1. Total standard catch of megalopae by month.

northern Gulf. More (1969) and King (1971) reported a February-March peak of *Callinectes* spp. megalopae and suggested these megalopae represented an overwintered spawn from the previous fall. While a February-April peak of portunid megalopae was also observed in the present study, it consisted almost entirely of *C. similis* and *Portunus* spp. Adkins (1972) also reported a February peak of blue crab megalopae from Whiskey Pass, Louisiana. Portunid megalopae and early crabs collected from this same site during February and March 1981 were provided to the authors by Mr. Adkins. All were found to be *C. similis*. Perry (1975) also reported a February occurrence of *C. sapidus* megalopae based on identification of young crabs reared from megalopae. Subsequent examination of these crabs found them to be *C. similis*. Abundance of *Callinectes sapidus* megalopae during the late spring through fall months observed in the present study is in general agreement with previous studies.

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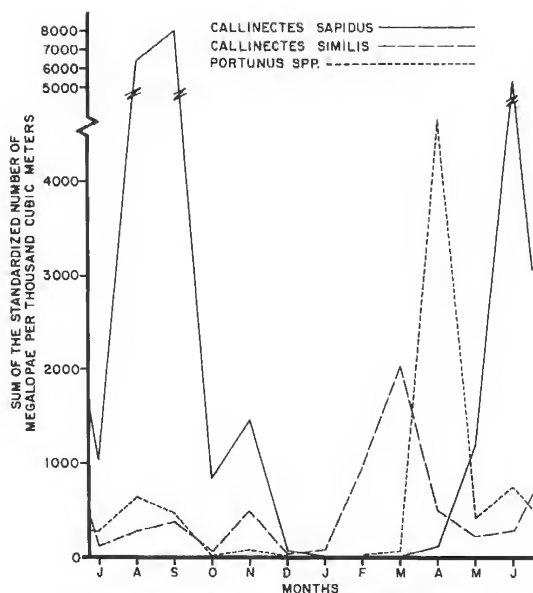
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